Using a multiproxy analysis of springbok fossils to track 2 million years of vegetation changes experienced by hominins in southern Africa

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Submitted in partial fulfilment for the degree of PhD

September 2018

Faculty of Science and Technology

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Front cover figure caption: Juvenile Antidorcas marsupialis from the Rhino and Lion Nature Reserve, Kromdraai, Krugersdorp, South Africa. [Photograph by L. Sewell, October 2017].

ABSTRACT

A causal link between climatic changes and hominin evolution is an established one, yet the exact dynamics of this relationship is debated. Key climatic changes, such as the intensification of the Northern Hemisphere Glaciation, the onset of the Walker Circulation and the Mid-Pleistocene Revolution, have been linked to palaeoenvironmental changes that catalysed hominin evolutionary events in Plio-Pleistocene Africa. Climate-induced faunal turnover has not been found in East Africa, largely due to local buffers of large-scale climatic and environmental changes. Away from the dynamic landscapes of East Africa, southern Africa is thought to be more vulnerable to the effects of climate change.

Southern Africa, as a major locale of hominin evolution and associated behavioural advancements, (with the appearance and disappearance of *Australopithecus africanus*, *Australopithecus sediba*, *Paranthropus robustus* and the emergence the *Homo* genus) requires greater understanding of the underlying catalysts for paleoenvironmental change and resultant pressures subjected upon the fauna (including hominins). A holistic palaeoenvironmental and palaeovegetational context for these hominin advancements remains elusive. This research aims to contribute to that holistic palaeoenvironmental signal for southern Africa between 2.0 to 0.8 Ma.

As herbivorous, mixed-feeding antelopes, the abundant springbok (genus *Antidorcas*) adapt their diet according to the prevailing vegetation conditions. Via a multi-method analysis of *Antidorcas* diets, this enables inferences to be made regarding the prevailing palaeovegetational trends and habitat availability in the landscape, through this crucial temporal period.

In this thesis, the taxonomic identity of the *Antidorcas* genus represented at the Cradle of Humankind is initially established. *Antidorcas* dental specimens from multiple hominin sites in South Africa from the temporal range, 2.8-0.8 Ma, are subject to a multi-method analysis. Dental metrics allow inferences into *Antidorcas* phylogenetic adaptations and establishes the baseline of dietary capabilities. Dental use-wear analysis provides the lifetime (mesowear) and end of life (microwear) dietary signals, supplemented by the early years signal from stable isotope analysis (carbon and oxygen). Further palaeoenvironmental conditions, such as precipitation levels (oxygen isotopes) and exogenous grit/dust particles (use-wear) is inferred from use-wear and isotope analysis.

This research concludes that there is limited evidence for the presence of *A. australis* as a distinct species in the fossiliferous deposits of the Cradle of Humankind. All *Antidorcas* species show mixed-feeding dietary preferences through time, with the ancestral, *Antidorcas recki,* tending more towards browsing and *Antidorcas bondi* showing some tendencies towards grazing.

Antidorcas display no obvious turnover point within the lineage but rather gradual adaptation and speciation. An underlying palaeoenvironmental trend of increased aridity and open grasslands is apparent with a marked shift around c. 1.7 Ma. Around 1.7 Ma *Antidorcas* dietary changes display high inter- and intraspecific variation, implying increased palaeoenvironmental instability and habitat heterogeneity. These behavioural adaptations (via dietary inferences) coincide with climatic changes around 1.7 Ma, such as the onset of the Walker Circulation. This in turn may be linked to the appearance of the southern African *Homo* genus and associated hominin Acheulean toolkit.

Table of Contents

LIST of TABLES

List of Illustrations

Appendices Contents (digital)

Accompanying material:

- Digitised appendices
- Publication to date from this research (electronic version)

I dedicate this thesis to my ever-supportive friends and family, without whom none of this would have been possible, any success I have had, is because of you all.

"…Though silent is the fading light, the evening changes into night."

(Lawrence George Watts, an inspiration throughout my life and my motivation these last 10years).

ACKNOWLEDGEMENTS

Firstly, I would like to thank my supervisory team for their invaluable feedback, support and guidance: Sally Reynolds, Ellen Hambleton, Matthew Bennett and John Stewart. Thank-you to my thesis examiners, Dr Fiona Coward and Professor Sarah Elton.
I would also like to thank my collaborators and their respective research institutes: Bernhard Zipfel (Evolutionary Studies Institute, University of the Witwatersrand)), Gildas Merceron (Laboratoire de Paléontologie, Évolution, Paléoécosystems, Paléoprimatolgie (PALEVOPRIM), Université de Poitiers) and Philip Hopley (Birkbeck, University of London). Thank-you for your assistance, hospitality and particularly your expertise, this research could not have been completed without any one of you.
My gratitude goes to the following for allowing access to their collections and their assistance throughout my visits: At the Ditsong Museum of Natural History, Pretoria: Stephany Potze, Lazarus Kgasi, Heidi Fourie, Miriam Tawaine. At the ESI, University of the Witwatersrand, Johannesburg: Bernard Zipfel, Thank-you also for your generous hospitality and assistance throughout. Thank-you also to Marion Bamford for guidance on phytolith sampling, to Christine Steininger for introducing me to the Cooper's Cave collections and thank-you to Francis Thackeray for taking time to talk to me about your research and to present my ideas at the SASQUA conference on our behalf At the National Museum of Scotland, Edinburgh: Zena Timmons and finally at the Natural History Museum, London: Roberto Portela Miguez.
I would also like to thank colleagues at these institutions who went out of their way to make me feel welcome.
Thank-you to Genevieve Dewar and Ben Collins, whose advice before my PhD I carried through, thank-you also for offering advice and suggesting contacts.
At Bournemouth University, Thank-you to Steve Smith, Bournemouth University IT Skills for invaluable guidance with SPSS and Adobe photoshop. Thank-you also to Emma Jenkins for phytolith assistance, to Paul Hartley for Leica microscope training, Damian Evans for discussing ideas and experimenting with casting alternatives.
Thank-you to the willing participants in my mesowear experiment, listed here and to those who chose to remain anonymous: Emily Barcham, Anna Gaston, Pip Rackstraw, Lewis Hua, Jen Vaughan, Jennie Mills, Dan Mills, Emily New, Jack Coles, Ruth Ditch, Nadine Wright, Rosemarie Wachsmuth, Ellen Hambleton, Kelly Sinclair, Eileen Watts, Julie Sewell, Paul Sewell, Martyn Sewell, Rosemary Powell, Daniel Powell, Rupert Cope, Penelope Foreman, Ashley Green, Richard Mikulski, Oxala Garcia Rodriguez, Hannah Haydock, Michelle Feider, Kelly van Leeuwen, Matt Stone, Paul Clarkson.
Thank-you to Pip Rackstraw for being on standby as a research assistant, I'm sorry we didn't get to go.
A special thank-you must be given to Lucile Crété, without whose assistance on the second data collection trip to South Africa, discussion of ideas and general friendship, I could not have completed this research! Thank-you also to Antoine Brémond for offering assistance.
Thank-you to my fellow postgraduate researchers at Bournemouth University, especially to my fellow office mates; Shannon Birch, Paul Evans, Tadhg Caroll, Penny Foreman and Lucile Crété for being on hand for assistance with various things and keeping me sane and to my coffee break buddies, Kelly van Leeuwen, Ailidh Barnes and Lucile Crété.
My gratitude goes to Ruben Lavooij, Paul Sewell and Confidence IT for salvaging lost and corrupted documents!
I cannot thank the following fantastic friends enough for taking the time to proof-read my chapters without questioning: Anna Gaston, Anna Gausden, Emily Barcham, Emily New, Jennie Mills and Laura Jones.
And finally, a massive Thank-you to Rupert Cope, firstly for his assistance at the initial data collection trip to South Africa, and taking hundreds of photographs. Secondly, for his unwavering support throughout and thirdly, for convincing me to get two beagles, who make any day that much easier.

FUNDING This research was completed as part of a Bournemouth University funded studentship, with the additional aid of grants from the following institutions:

BIEA (British Institute in Eastern Africa), to allow travel to South Africa for data collection (2017).

The Palaeontological Association small travel grant, to present the preliminary results of this research at the Open Science Meeting PAGES International Conference, Zaragozza, Spain, 2017 and a second small travel grant aspects of this research at INQUA 2019 in Dublin, Ireland.

The Prehistoric Society Coles Award and collaboration with the institute*, to complete microwear analysis at the *Laboratoire de Paléontologie, Évolution, Paléoécosystems, Paléoprimatolgie (PALEVOPRIM; ex-iPHEP), Université de Poitiers, France.

DECLARATION

Data collected in 2016 (as highlighted in Appendix A10) was partly used in the following previous publication (published as a result of this PhD research).

Sewell, L., Merceron, G., Hopley, P.J., Zipfel, B. and Reynolds, S.C., 2019. Using springbok (*Antidorcas*) dietary proxies to reconstruct inferred palaeovegetational changes over 2 million years in Southern Africa. *Journal of Archaeological Science: Reports* 23, 1014-1028.

GLOSSARY OF TERMS

AAC: Alcelaphine+Antelopini criterion (Vrba 1974, 1975, 1980)
Breccia: Calcified or decalcified cave infill.
Chronospecies: a species derived from sequential evolution (i.e. no sister taxa)
Evolutionary events: Speciation: (first appearance of a new species), extinction (last appearance of a species) and migration (immigration/emigration of a species from/to an area).
ENSO: El Niño Southern Oscillation
El Niño: Temporary climatic event, characterised by unusually warm temperatures and reversal of wind patterns and unseasonal rains. The warm phase*.
FAD: First Appearance Datum (oldest known appearance of the species)
Inter-specific: Between species
Intra-specific: Within species
iNHG: intensification of the Northern Hemisphere Glaciation
Karst: Topography formed from the dissolution of soluble limestone rocks.
LAD: Last appearance Datum (last known appearance of the species prior to extinction).
La Niña:As El Niño but less severe and occurring less frequently, the cold phase*.
Lineage: a continuous species (e.g. fossil *Antidorcas marsupialis* to extant *Antidorcas marsupialis*). Here, a lineage is taken to show the ancestral, fossil and modern forms, i.e. *Antidorcas recki* (ancestral), fossil *Antidorcas marsupialis* and extant *Antidorcas marsupialis*.
LGM: Last Glacial Maximum
Member: Cave deposit stratigraphic unit
MPR / MPT: Mid-Pleistocene Revolution / Mid-Pleistocene Transition
oWC: onset of the Walker Circulation
Palaeoecology: Diet and ecology of fossil species
Palaeohabitat: Inferred habitats available within the landscape or an area inhabited by fossil species
Palaeoclimate: Past climate
Palaeoenvironment: Past environmental conditions
Palaeovegetation: Past vegetation (Flora, all plants, including tress and grasses)

Speleothem: Cave precipitate
Uniformitarianism: Using extant / modern species to inform on the genera/ species in the past, assuming they yield the same characteristics.

Vegetation

See Appendix A2.

C_3: Plants using the Calvin cycle / C_3 photosynthetic pathway to fix carbon. Typically trees and shrubs found in wetter, more humid areas.
C_4: Plants using the C_4 photosynthetic pathway, prevailing in cooler, more arid environments, typically grasses.
CAM: Crassulacean acid metabolism. Typically grow in arid conditions, using both the C_3 and C_4 photosynthetic pathway.

Dietary Ecologies

Browser: Herbivore consuming predominantly C_3 dicotcotyledonous plants, including trees, seeds, fruits and shrubs.
Dicot: Flowering plants (angiosperms) with two cotyledons (embryonic leaves)
Grazer: Herbivore consuming predominantly C_4 monocotyledonous plants, such as grasses,
Monocot: Flowering plants (angiosperms) with one cotyledon (embryonic leaf)

Dates

ka: Thousand years ago
Ma: Million years ago
Pliocene: c. 5.33-2.58 Ma
Pleistocene: c. 2.58- 0.01 Ma
Plio-Pleistocene: Geological time period at the boundary of the Pliocene and Pleistocene epochs (Stratford 2018). It is the sixth epoch of the Cenozoic era and the first epoch of the Quaternary period. The end of the Pleistocene corresponds to the end of the Palaeolithic.

Date	South African term	Epoch
3.4Ma-300,000ya	Early Stone Age (ESA)	Pliocene/Pleistocene
280,000-50,000ya	Middle Stone Age (MSA)	Pleistocene
50-39,000ya	Late Stone Age (LSA)	Holocene

Taxonomy

As there is considerable debate regarding the taxonomic identification of certain specimens, a debate which is beyond this research, I summarise the species referred to here.
-***Homo erectus***: as referred to throughout this thesis refers to *Homo erectus senso lato*.
-***Homo erectus* (*senso lato*)**: African and Eurasian '*Homo erectus*'
-***Homo erectus* (*senso stricto*)**: Asian '*Homo erectus*'
-***Homo ergaster***: African *'Homo erectus'*
-***Paranthropus robustus*** is alternatively referred to in published literature as *Australopithecus robustus* or the southern African robust Australopithecines

Method specific glossary

DMTA: Dental Microwear Texture Analysis
Asfc: Area-scale fractal complexity
EpLsar: Exact proportion length scale anisotropy of relief
HAsfc: Heterogeneity of area-scale fractal complexity, measured at varying scales (such as those used here, of 3 squares by 3 squares (3x3) is 9 cell, 9 by 9 (9x9) is 81 cell
Tfv: Textural fill volume
Smc: Scale of maximum complexity
Abrasion: Food (or particle) to tooth contact
Attrition: Tooth to tooth contact
Cusp shape: Shape of the molar cusps
Relief: Relative occlusal relief of the molar cusps
Mesowear Score: Numerical scale combining cusp shape and relief attributes

New Mesowear Score, New relief, New cusp shape: Mesowear scales and parameters trialled in this research (see chapter 11)
Buco-lingual (BLW): the width of the molar, taken across the occlusal surface (outside of mouth to the inside of the mouth)
Mesio-distal (MDL): the length of the molar, taken across the occlusal surface (if of M2, from the first molar edge to third molar edge)
Crown height (CH): The enamel covered part of the tooth, visible above the gumline
Occlusal height (OH): Measured height of the molar cusps
Total height (TH): Total height of the molar from root to cusp

Anatomical terminology

M^1: Upper permanent (adult dentition) first molar (i.e. adult maxillary dentition).
M_1: Lower permanent (adult dentition) first molar (i.e. adult mandibular dentition).
M2: Permanent second molar
UM2: Upper permanent second molar
RUM2: Right upper permanent second molar
LLM2: Left lower permanent second molar
Pm: pre-molar
Buccal: Outer edge of the tooth surface next to the cheek
Distal: Surface of the tooth towards the back of the mouth
Lingual: Inner edge of the tooth surface, next to the longue
Mesial: Surface of the tooth towards the front of the mouth
Occlusal: Biting surface of the tooth, that comes into contact with the opposing teeth when chewing / grinding

Site and assemblage acronyms

CoH: Cradle of Humankind
SK: Sterkfontein
SKX: Swartkrans
K: Kromdraai
GD: Gondolin
CC: Cooper's Cave
PL: Plovers Lake
COH: Cave of Hearths
GL: Gladysvale
DMQ: Drimolen Main Quarry
M: Member
M5W: Member 5 West
PM6: Post-Member 6

CHAPTER 1

INTRODUCTION

The Plio-Pleistocene in southern Africa was a centre of hominin evolution. This epoch heralded the emergence and disappearance of several hominin species in East and South Africa. For South Africa, this epoch witnessed the appearance and disappearance of *Australopithecus africanus*, *Australopithecus sediba*, *Paranthropus robustus* and eventually the emergence of the *Homo* genus. Causally related to the appearance of the *Homo* genus, was the advent of new stone tool technologies and other associated behavioural advancements, such as the controlled use of fire.

These great changes and advancements in hominin adaptations seen during the Plio-Pleistocene have been investigated via a plethora of methods that have been implemented and continually refined. These include but are not limited to: hominin-cercopithecoid comparisons (e.g. Jolly 1970; Elton 2000; Beaudet et al. 2016; Gilbert et al. 2016); analysis of tool use (e.g. McHenry 2018); and palaeoenvironmental influences via bovids (e.g. Vrba 1985, 1988; Spencer 1997), carnivores (e.g. Kuhn et al. 2017), micromammals (e.g. Avery 2001); and climate (e.g. de Menocal 1995, 2004; Lupien et al. 2017; Quinn 2017).

Pliocene and Pleistocene climate transitions are theorised to have led to cooling, drying trends that resulted in the spread of grasslands and the shrinking of forests (e.g deMenocal 1995, Spencer 1995, Lee-Thorp et al. 2007). This, in turn, is hypothesised to have led to major changes in the structure of the inhabiting faunal community (e.g. the Pulse Turnover Hypothesis proposed by Vrba 1985). Ultimately, these variations have been implicated in the major changes (tool use, brain size increase) and associated behavioural advancements seen at the emergence of the *Homo* genus (e.g. Dart 1925; Hopley et al. 2007).

The National Research Council (US) (2010) identified that how climate has shaped hominin evolution is a key knowledge gap, encouraging research for understanding the potential impact of climate change contemporaneously and in the future. This research addresses that gap in southern Africa. In order to adequately address this gap, there are numerous factors to consider.

The palaeovegetation of a landscape is shaped by a combination of factors, including climatic and environmental conditions, hydrological factors, geology, topography, altitude and soil matrix. Climatic conditions are believed to be the prevailing influential factor dictating the palaeovegetation cover of the area (e.g. Cerling et al. 1997). Any palaeovegetational changes then influence faunal adaptations in southern Africa. The extent of this link is currently disputed. From the savannah hypothesis (Dart 1925), to Vrba's highly influential Pulse Turnover Hypothesis (1985) to Potts' Variability Selection Hypothesis (1998) and the relatively recent Pulsed Climate Variability Hypothesis (Maslin et al. 2015), the link between climate change and faunal evolution is debated. What were the palaeoenvironmental and vegetational conditions and changes therein that occurred in southern Africa in the Plio-Pleistocene between 2.8 and 0.8 Ma? And how did this impact on the faunal community inhabiting the landscape? Establishing this palaeovegetational backdrop will allow us to infer the environmental changes and impact of climatic stimuli the resident faunal community (including hominins) were subject to.

Limited botanical or palynological remains are preserved in South Africa (but see Bamford 1999, 2015; Bamford et al. 2010), particularly in the cave deposits where the majority of the Plio-Pleistocene hominins are found. Bamford (2015)'s macrobotanical evidence from Wonderwerk Cave (Northern Cape Province, South Africa) from 2 Ma to 14 ka provides some of the only direct floral evidence of vegetation present throughout this crucial time period in hominin and faunal evolution. However, evidence of this kind remains scarce within the geographical range of the Cradle of Humankind, (Gauteng Province, South

Africa) where the majority of hominin remains are found to date. There are multiple vegetation biomes present across South Africa today and it should not be assumed that the Plio-Pleistocene vegetation in the Gauteng Province would match that identified from the Northern Cape.

In light of the limitations from the direct botanical evidence, utilising the bovids that consume the vegetation is a viable alternative palaeovegetation indicator. Using palaeovegetational indicators to understand faunal (including hominin) turnover is an established connection. Bobe and Behrensmeyer (2004) for instance, highlight the long-held link between palaeovegetation, palaeoclimate and hominin evolution, discussing the grassland expansion, driven by global climatic changes, leading to divergence in the hominin lineage. There is likely to be a lag effect from climatic changes to climatically-induced vegetation changes and, subsequently, for vegetation-change induced faunal changes. Therefore, any changes seen within a relatively short timeframe after known climatic events can be considered to have been potentially catalysed by the preceding climatic change. Fossil bovids specifically, are widely recognised as valuable ecological indicators due to their representation of the entire vegetation spectrum from specialised, through mixed-feeding taxa, to specialised browsers. Their use in palaeoenvironmental reconstructions associated with the hominins of Africa is proven (e.g. Gentry 1970; Vrba 1985; Spencer 1997; Reed 1998; Hernández Fernández 2001; Luyt 2001; de Ruiter et al. 2008a; Steininger 2011; Brophy et al. 2014).

To establish the palaeovegetation of the area, the dietary signals from the springbok, genus *Antidorcas* are used here. *Antidorcas* was an abundant herbivorous antelope genus present throughout this time period, and a reliable reflector of the available vegetation. As much of the bovid fossil record (and, therefore, palaeovegetational indicators) is represented by isolated dentition (e.g. Brain 1981; Brophy et al. 2014), multiple diagnostic methods are implemented to more precisely determine dietary ecologies of fossil specimens.

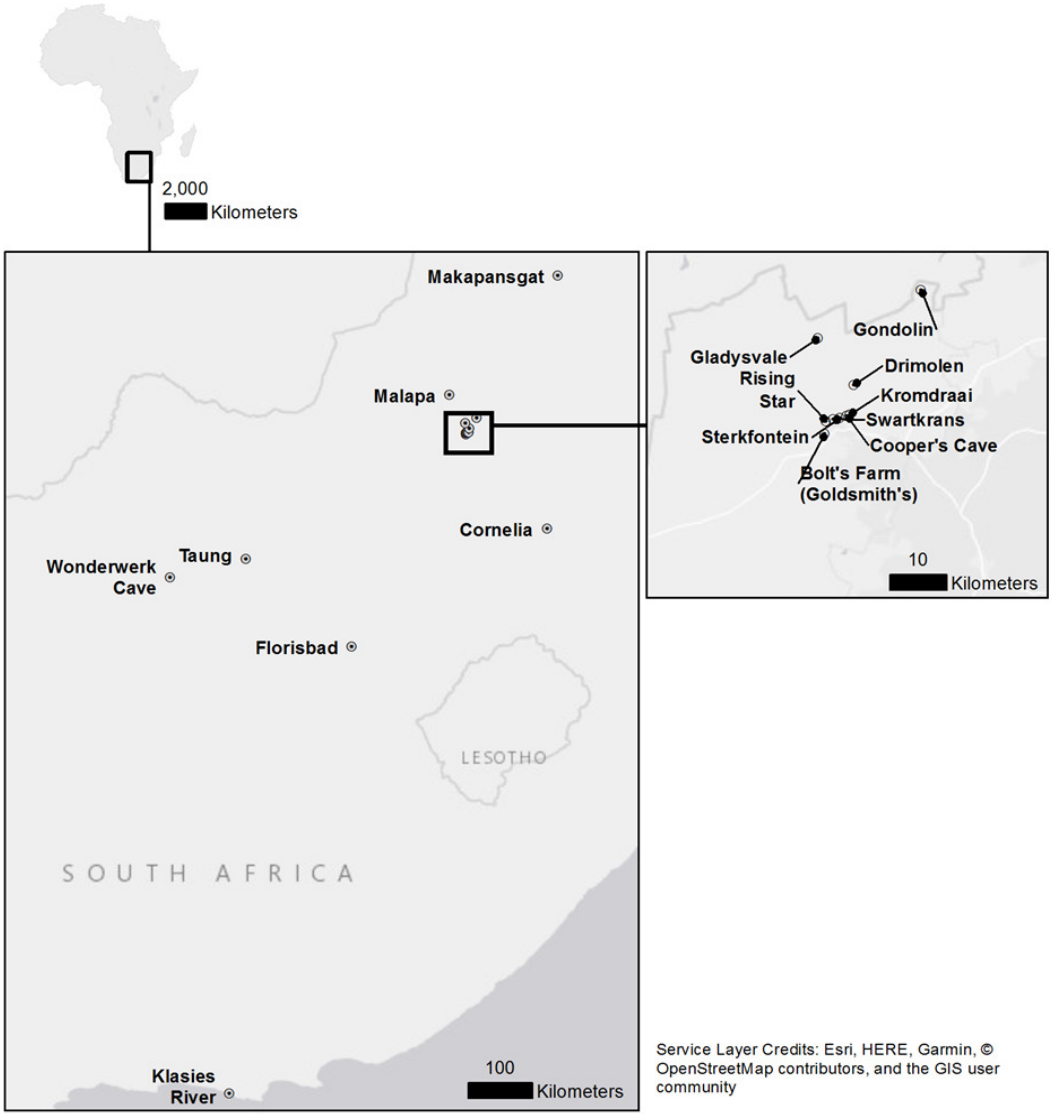


Figure 1.1. Map of South African key hominin-bearing fossil site locations indicated (left), with a focus on the Cradle of Humankind (right). Map created by L. Crété.

With the limitations in mind, the knowledge gap of the palaeoenvironmental backdrop to hominin evolution can be addressed in southern Africa, with the following research questions.

1.1 RESEARCH QUESTIONS

1) What was the prevailing landscape vegetation cover and aridity like in southern Africa between 2.8-0.8 Ma?
2) What was the extent and tempo of vegetation and faunal change? Do these changes relate to known global climatic trends and events (if so, how), and how do these changes relate to prevailing evolutionary hypotheses (e.g. Vrba's (1985) turnover pulse hypothesis)?
   -Are there any major evolutionary events or dietary shifts seen in the *Antidorcas* lineage?
3) What was the palaeoecology of the *Antidorcas* species?
4) What can *Antidorcas* information gained here add to the hominin story?

1.1.1 Aims and objectives

Table 1.1 Aims and objectives of thesis.

AIMS	OBJECTIVES
Reconstruct the palaeovegetation in southern Africa between 2.8-0.8 Ma	Interpret the diet of *Antidorcas* species through time via use-wear analysis and stable isotope analysis.
	Interpret the hydrological changes through time via stable oxygen isotope analysis.
Evaluate the *Antidorcas* genus and lineage, taxonomic identifications and palaeoecology	Dental morphological measurements, is there a directional change through time?
	Behavioural change is inferred from dietary shifts.
	Establish the likely dietary preference for each *Antidorcas* species via use-wear and stable isotope analysis.
Evaluate the catalysts and drivers of hominin and faunal evolution in southern Africa	Compare *Antidorcas* data to known climatic events
	Compare *Antidorcas* data to evolutionary hypotheses (e.g. Vrba's TPH)
	Compare Antidorcas data to known hominin trends, particularly across the Oldowan-Acheulean transition in southern and East Africa.
Evaluate the methods used and the value of a multi-method analysis for detailed palaeoenvironmental reconstructions.	Consider what each method informs on for the palaeoenvironment.
	Combine the results from each method. Does this give a more holistic picture, can we learn more than from the individual methods?

1.2 RATIONALE

The diet of fossil springbok (*Antidorcas*) will be used to infer the palaeovegetation of southern Africa between c. 2.8-0.8 Ma. *Antidorcas* dental morphology is measured to assess consistent morphological changes potentially indicating *Antidorcas* lineage turnover. *Antidorcas* dietary evidence available from dental specimens (via use-wear, and isotope analysis) is used to infer likely prevailing vegetation cover, highlighting when and if any changes within this vegetation cover take place during this temporal period in South Africa.

Then the inferred palaeovegetation coupled with any lineage changes within the *Antidorcas* genus will be compared to known climatic data; obtained from marine (e.g. deMenocal 1995, 2004, 2011) and terrestrial (e.g. from speleothems Hopley et al. 2007, 2009) sources.

Oxygen isotopes provide an insight into aridity levels. Dietary morphology shows the long-term, ancestral dietary capabilities, with reference to ancestral dietary adaptation-inducing stressors. Individual animal lifetime dietary signals (short-term, vegetation presence indicator) are indicated by dental use-wear and dental enamel carbon isotope values.

The palaeoenvironmental picture obtained from established research and information gained here, from *Antidorcas*, will subsequently be used to infer the palaeoenvironmental conditions experienced by southern African hominins. Particular attention will be paid to dates of believed hominin adaptation and advancement.

This research aims to provide an environmental and vegetation context within which to postulate how climate and habitat changes may have affected hominin evolution in South Africa. The multi-proxy approach produces robust measures of habitat conditions and allows inferences to be drawn about the forces that shape evolutionary processes in humans and other mammals. The relatively recent discoveries in South Africa of *Australopithecus sediba* (Berger et al. 2010) and *Homo naledi* (Berger et al. 2015) further underline the need for more research on such fossil collections: our understanding of the hominin evolutionary trajectory is itself ever-evolving. This palaeoenvironmental research aims to increase both scientific and public understanding of human evolution and survival in southern Africa between 2.8-0.8 Ma. How hominins adapted to varying climatic stimuli will be of considerable use to the scientific community studying human evolution from any time period anywhere in the world.

Antidorcas dentition as a bioproxy for vegetation change

Antidorcas dietary change (as evidenced by use-wear analysis and stable carbon isotope values from dental enamel), is indicative of vegetation change. Using a relatively continuous chronology of *Antidorcas* dentition, a chronological sequence (spanning 2 million years) of prevailing vegetation from the Cradle of Humankind can be drawn. Supplementary species (*Damaliscus pygargus* and *Tragelaphus strepsiceros*) are used to establish the grazing-browsing parameters for each time-period represented by assemblages within this temporal range.

Rationale for using springbok

To investigate the nature and extent of 2 million years of palaeovegetation and palaeohabitat changes across the landscape; an herbivorous, mixed-feeding genus (fossil springbok) is used. Because the springbok has evolved successfully throughout the temporal period under study, it can be presumed that their ability to vary their diet in accordance with the prevailing vegetation enabled their success. Analysing the dental enamel traits (enamel thickness, mesowear, microwear and stable isotope analysis) enables a reconstruction of the likely diet, in order to extrapolate differential proportions of vegetation around the Cradle of Humankind during the 2.8-0.5 Ma period (The temporal range is partially extended for *Antidorcas* palaeoecology investigations beyond 0.8 Ma due to the prevalence of *Antidorcas* at slightly younger, related sites, such as the Cave of Hearths).

Antidorcas yields a more abundant fossil record than hominins from the same deposits, from which to interpret palaeoenvironmental changes. A more abundant taxa enables larger sample sizes to be studied, and the implementation of destructive techniques, such as stable isotope analysis (C_3/C_4 vegetation dominance, habitat types supported and hydrological information) in the landscape, shared by hominins and their faunal community, of which *Antidorcas* was a part.

Hominins are believed to have been omnivorous (e.g. Lee-Thorp et al. 1994; Sponheimer et al. 2005), clouding the palaeovegetational signal. The data gained from this research will be corroborated with published hominin data to further understand how hominins fit into this

palaeoenvironmental picture. As mixed-feeding herbivores, *Antidorcas* can give a more faithful reflection of the palaeovegetation conditions than would be possible via hominin fossils. The dietary niche of an animal species is influenced by (and therefore reflective of) the local quality, quantity and accessibility of available resources (Lehmann et al. 2015). Dietary niches of populations are expected to expand and contract in response to the availability of the animals preferred food items (Codron et al. 2007; Owen-Smith et al. 2013). Obligate grazing / browsing species may be intermittently present / absent from the fossil record, likely as a reflection of the presence / absence of their preferred vegetation type. As a mixed-feeding species, capable of adapting its diet to the prevailing vegetation, *Antidorcas* is continuously present throughout. This mixed-feeding species is therefore likely to be a faithful bioproxy, reflecting the changeable availability in a wide array of vegetation types supported by the given environment of the time.

Antidorcas is also found in great abundance in the other centre of hominin evolution, in East African fossil faunal assemblages and hominin contexts. The ancestral *A. recki* is found in East African contexts such as Lake Turkana (Kenya) and the Omo valley (Ethiopia) between ~3.36-1.6 Ma (Harris 1991; Brugal et al. 2003), as well as Olduvai Gorge (Tanzania) up to ~0.8 Ma (Bed IV) (Gentry and Gentry 1978). Thus, should *Antidorcas* prove to be a faithful bioproxy, there is potential to use their remains in other areas / periods significant to our understanding of human evolution.

Rationale for using fossils from southern Africa

Australopithecus, Paranthropus and *Homo* are present in both East and South Africa between 3-0.5 Ma. Yet their species differ (*Australopithecus afarensis, Paranthropus boisei and aethipicus* in East Africa). Towards the latter end of this temporal range, *Homo* is found in sites outside Africa, such as Dmanisi (Georgia) (Gabunia et al. 2000) and Atapuerca (Spain).

It is believed that hominin sites in East Africa were buffered from major climatic and environmental changes by regional factors such as dynamic landscapes with palaeolakes and ongoing tectonic activity (i.e. the Tectonic Landscape Model or 'TLM' (Bailey et al. 2011; Reynolds et al. 2011)). Contrastingly, this influence of such large-scale buffers on landscapes is believed to be considerably lower in southern Africa. Thereby, making southern Africa more vulnerable to global and regional climatic and environmental factors, and potentially ensuring them as the main drivers of hominin evolution.

Thus, in southern Africa, climatic conditions are believed to be the primary influencing factor dictating the palaeovegetation present (e.g. Reynolds 2007; Vrba 1985; deMenocal 1995). Southern Africa should show the impact of these global climatic trends to a far greater extent than in East Africa, where signals may be further mediated by multifaceted influences of dynamic, tectonically active landscape processes that modify regional environments (Reynolds et al., 2011). Work in East Africa has not shown to be in line with Vrba's Turnover pulse hypothesis, as no major 'pulses' (faunal evolution co-occurring in multiple species within a short time frame) were detected (Bibi and Kiessling 2015). There is the possibility that the pulses were an artefact of the fossil record and of taxonomic

uniformitarianism assumptions (e.g. Maxwell et al. 2018; Lee-Thorp et al. 2007). Therefore, the question of the pace and severity of evolution and its drivers remains pertinent.

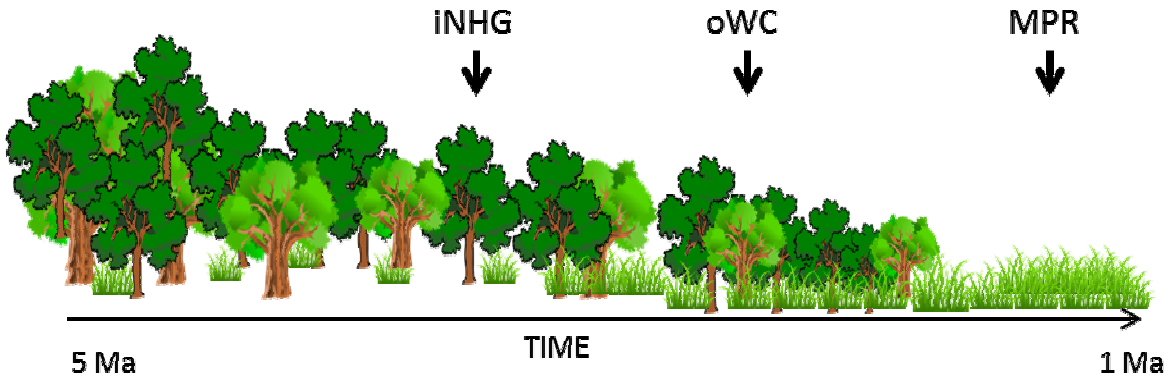
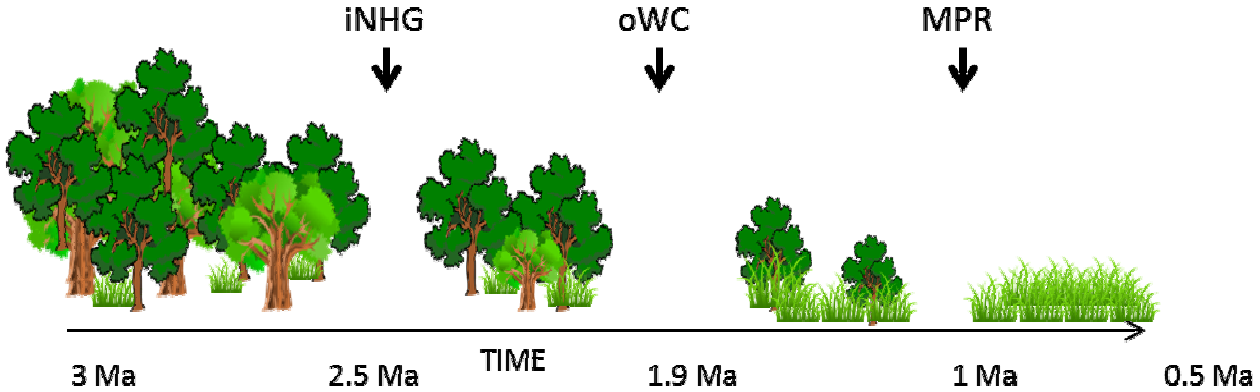
Assessing the role of climate as an evolutionary driver is crucial when attempting to understand the complexities surrounding hominin evolution. DeMenocal (1995) has shown the importance of understanding global climatic trends, which will be addressed in this research. Amongst others, DeMenocal (2004; 2015) showed causal links between climatic events and evolutionary events, as will be discussed in later sections. Yet, further conclusive research is required to truly understand the nature of climate's role as an evolutionary driver. Published climate data will be used in corroboration with the palaeovegetation data gained from this research to better understand the role of climate as an evolutionary driver.

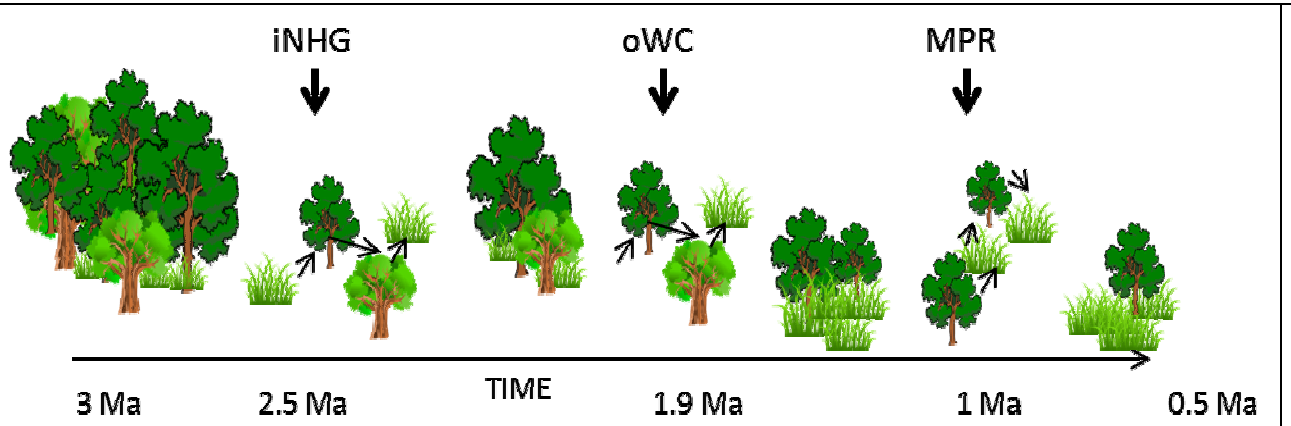
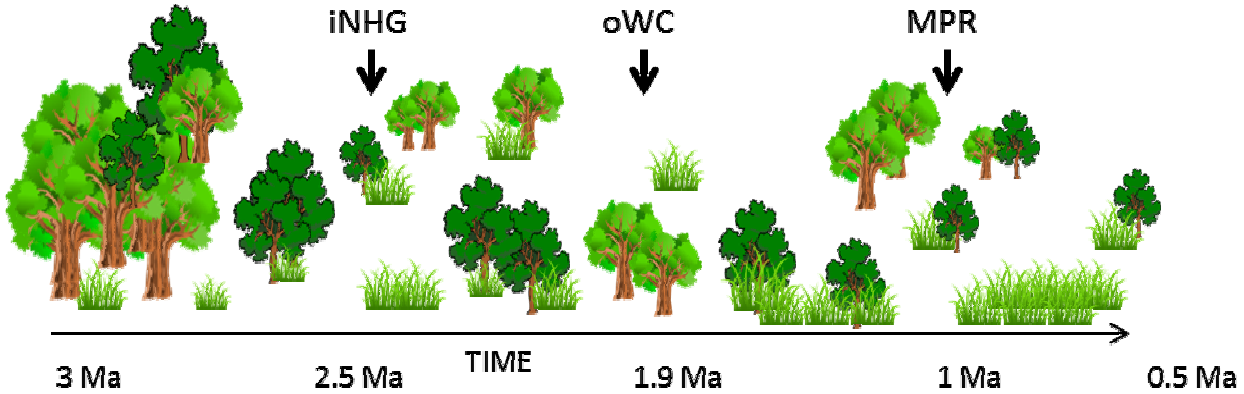
1.3 HYPOTHESES

Evolutionary hypotheses are explained in detail in the following chapter. A selection of the ones deemed most relevant to this research are explored here, hypothesising what may be expected of the *Antidorcas* data obtained in this research to satisfy each hypothesis.

Expanded explanation of hypothesis Figure 1.2: The arrow along the bottom represents time from 3 Ma to 0.5 Ma, with major climatic events added (these are explained in full in chapter 2), with coloured vertical bars (iNHG = intensification of the Northern Hemisphere Glaciation; oWC=onset of the Walker Circulation; MPR=Mid-Pleistocene Revolution). The size of the springbok represents their relative dominance (blue-grey horizontal bar),. *A recki* is the more abundant springbok at 3 Ma, *A. bondi* (green) is the most abundant c. 1.7 Ma and *A. marsupialis* (extant springbok) slowly becomes the most dominant springbok form. Above this, the springbok genus is depicted with *A. recki* represented by a red line, *A. marsupialis* by blue and *A. bondi* by green. Potential habitat evolution is shown above (green-yellow horizontal bar), with a shift from C_3 to C_4 vegetation from 3.0 Ma to 0.5 Ma. Two possible scenarios are suggested, the climate-driven transition from woodland to grassland occurring rapidly and suddenly caused by climatic events (top vegetation scenario). Alternatively, climate is buffered by local and regional factors (bottom vegetation scenario), allowing habitat heterogeneity to persist through global climatic changes, with vegetation and subsequent *Antidorcas* evolution correspondingly more gradual. Southern African hominins are shown at the top, roughly aligned to their temporal range.

Table 1.2: Some of the key evolutionary theories (or hypotheses) and their proposed vegetation changes, in response to global climatic events and how each would manifest in the Antidorcas evidence achievable from this research. The 3 main global climatic events are indicated, with their impact on the vegetation according to each hypothesis (in the central column). The right column indicates how each of these scenarios would be apparent from the Antidorcas data.

Hypothesis	**Proposed environmental and vegetation change according to climatic stimuli**	***Antidorcas* evidence**
SH (savannah hypothesis) (Dart 1925)		C_4 vegetation dominance gradually replaces C_3-dominance over the temporal range ($\delta^{13}C$). Oxygen isotopes ($\delta^{18}O$) would show increased aridity through time. Increasing abundance of grazing signals from use-wear.
TPH (turnover pulse hypothesis) (Vrba 1985)		Not necessarily unidirectional through time but rapid evolution (pulse) (visible via dental morphology and species identification) shortly after a global climatic event.

VSH (variability selection hypothesis) (Potts 1998)		Environmental instability (visible via temporarily increased intra and inter-specific dietary variation (use-wear and stable carbon isotope analysis) within a Member) causes turnover (dental morphology and species identification).
MHM (mosaic habitat model) (Reynolds et al. 2015)		The relative components may change but 'micro-habitats' are continuously available (in varying sizes). This would be evidenced by no directional change apparent in dietary signals (use-wear and carbon isotopes) through time (presumably up to a threshold aridity level-visible through oxygen isotopes). Relatively high but constant intra- and inter-specific dietary variability would prevail. Habitats and species they support would be less affected by global climatic influences.

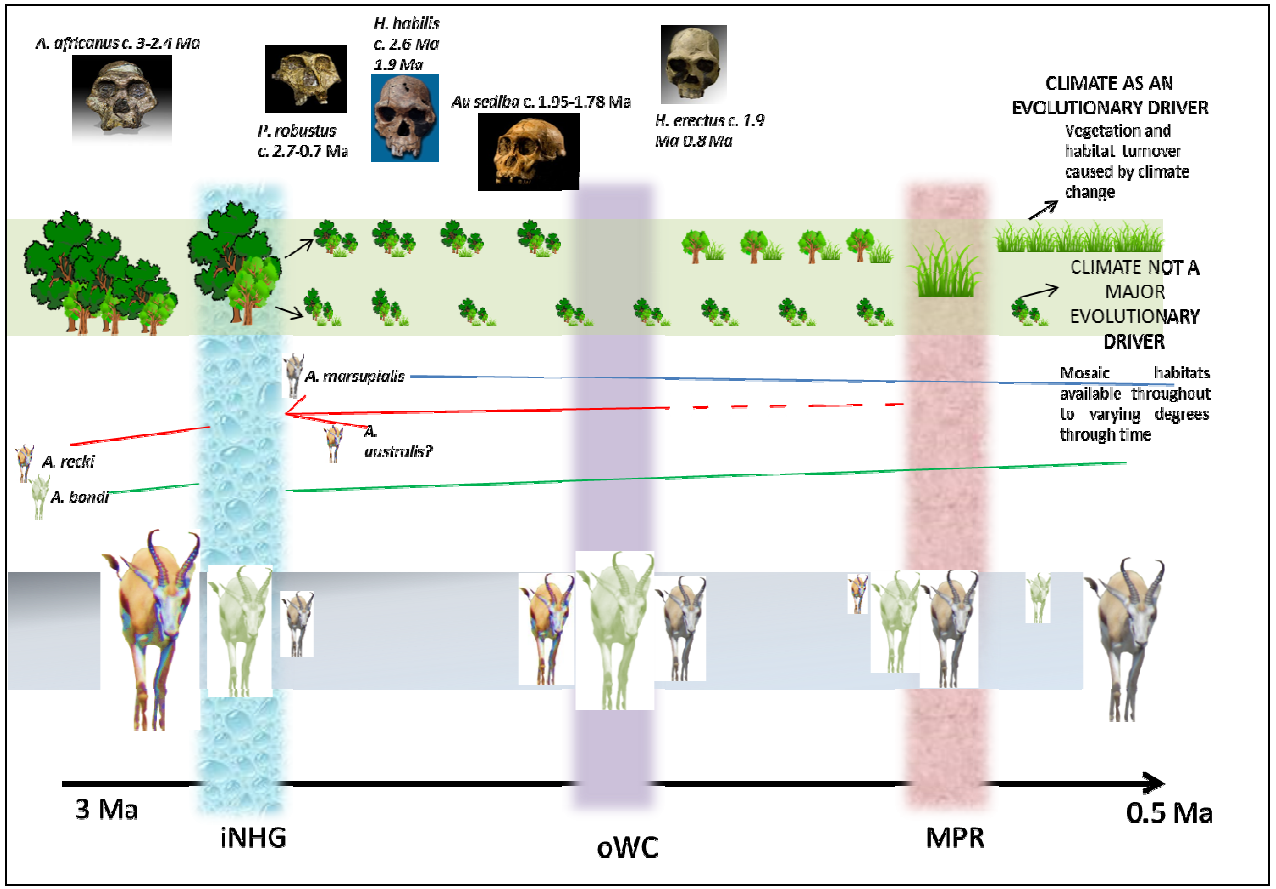


Figure 1.2 Hypothesised Antidorcas evolution and palaeoenvironmental changes as a response to climatic influences. The upper, green horizontal band shows dominant vegetation and the lower, grey, horizontal band depicts Antidorcas evolution. The size of the springbok represents relative abundance. See expanded explanation above.

1.4 RESEARCH METHODS STATEMENT

To address the research questions outlined above in section 1.1, the following methodological approaches will be taken. Each method is implemented on *Antidorcas* dental specimens from the same Member (site stratigraphic unit) provenance. Members are organised into relative chronological order to establish change through time (as detailed in 'Materials: sites' chapter).

- Dental morphological measurements are taken to establish the phylogenetic adaptive responses within the *Antidorcas* lineage and to assist in specifying, as far as possible, the taxonomic identity of each specimen. The measurements can also provide a starting point for dietary indicators, as dental morphology highlights the inherited dietary capabilities of an animal.
- Use-wear analysis of *Antidorcas* molars is implemented to establish the generalized lifetime diet of the *Antidorcas* individuals (mesowear) and a short-term snap-shot of the last few weeks of the *Antidorcas* individuals' life (microwear).
- Stable isotope analysis (carbon and oxygen) of selected *Antidorcas* molars allows an insight into the diet of young *Antidorcas* (during enamel formation and mineralisation), and potentially sheds light on the seasonality of their feeding preferences and preferential palaeohabitats. Oxygen isotope $\delta^{18}O$ values also give an indication of aridity levels and hydrological factors.
- [Phytolith analysis (in an attempt to gain direct evidence of vegetation present during the lifetime of that *Antidorcas* individual) from the dental calculus of *Antidorcas* molars forms the basis of ongoing work but falls outside the scope of the current thesis].

For each method, a selection of modern *Antidorcas marsupialis* dental specimens (see chapter 4) are subject to the same analysis as the fossil specimens, to predict the likely range of intraspecific variation within an *Antidorcas* species. A small subset of supplementary fossil species (*Damaliscus pygargus* and *Tragelaphus strepsiceros*) are also subject to the same analysis to establish the expected grazing (*Damaliscus*) and browsing (*Tragelaphus*) parameters for each cave deposit Member.

1.5 THESIS STRUCTURE

Following from this introduction, background into global climatic trends, the southern African palaeoenvironment and associated evolutionary theories and an introduction to the sites from which *Antidorcas* fossils originate is presented (chapter 2). The ecology and palaeoecology of the *Antidorcas* taxa is then summarised (chapter 3). This is followed by a chapter introducing the materials and methods used throughout this research (chapter 4). Background results follow: a meta-analysis of their faunal assemblages (chapter 5), The *Antidorcas* species taxonomic identifications are explored and a summary of modern *Antidorcas* data is provided (chapter 6) before fossil data is analysed. This is followed by the main data chapters (chapters 7-11), providing an analysis of *Antidorcas* insights into

southern African palaeovegetation. Each method implemented will be addressed in independent chapters, followed by a chapter combining all methods (chapter 11), which are drawn together prior to the overall discussion and conclusions (chapter 12).

The methods implemented with individual chapters are linear morphological measurements of *Antidorcas* dentition (dental molar volume and enamel thickness), use-wear analysis (mesowear and DMTA) and stable isotope analysis (carbon and oxygen).

CHAPTER 2

PALAEOENVIRONMENT OF SOUTHERN AFRICA 2.8-0.8 Ma and BACKGROUND TO THE CRADLE OF HUMANKIND SITES

Landscapes are vulnerable to fluctuating climatic and environmental factors from varying scales. At the largest scale, the global climate and environmental trends (such as ice ages) impact upon the landscapes, dictating many conditions and consequent vegetation and habitats the environment is able to support. On a smaller scale, regional environments (e.g. southern Africa to South Africa range) can be impacted to varying degrees depending upon the relative geology, soil matrix, tectonics, water sources and other features of the landscape, these regional scale variations can buffer or exacerbate global influences. At the local scale, (Gauteng province to Cradle of Humankind range) again differential buffers can exist, supporting vegetation across the region differentially according to local environmental and other abiotic influences. And at the smallest scale here, 'micro'- habitats (micro here refers to an area inhabitable by *Antidorcas*-sized animals) can further buffer or exaggerate the impact of the global, regional and local abiotic and biotic influences.

The key objective for this research is to add a novel approach contributing to the understanding of the environmental change that occurred and the catalytic impact of such environmental changes on faunal *(Antidorcas)* evolution. To achieve this, a temporal period in which faunal (including hominin) variability is apparent is required, as is a geographic region in which climate is believed to be one of the primary influencing factors, without conflicting buffers to their impact (e.g. palaeolake and, tectonic activity). The temporal period of 2.8-0.8 Ma in southern Africa undoubtedly experienced a period of environmental transition, but the severity, pace and variability of these changes are yet to be fully understood. By considering the believed climatic changes (published sources) that occurred, alongside the palaeovegetation indicators obtainable via herbivore (*Antidorcas*) dietary indicators during this temporal period, this research can extrapolate information

pertaining to the nature of the impact of these climatic changes on faunal and hominin evolution.

In this chapter, the area chosen to address this question (South Africa), is placed into context within Africa from the Plio-Pleistocene to Modern day. Global, regional and local factors are considered and the predicted evolutionary influencing climatic and environmental transitionary events are examined. The scale gradation of climatic and environmental impacts will be considered in turn. Attention will be given to the likely global climatic influences that catalysed faunal and hominin evolution. A brief discussion of the prevailing evolutionary theories is presented (and see Appendix A1) and previously proposed Plio-Pleistocene palaeoenvironments for southern Africa and specifically for the Cradle of Humankind are established.

BACKGROUND

Proposed evolutionary theories, such as Vrba's (1985) turnover pulse hypothesis (TPH) would see *Antidorcas* and hominins evolving in pulses, in response to global climatic changes (such as 2.7 Ma: Intensification of Northern Hemisphere Glaciation (iNHG); 2.0-1.7 Ma: Onset of the Walker Circulation (oWC); 1.0 Ma: Mid-Pleistocene Revolution (MPR)). Maslin et al.'s (2014) East African research was at odds with the TPH, suggesting that regional scale influences, such as tectonics (Reynolds et al. 2011; Bailey et al. 2011) created dynamic landscapes acting as buffers to these global influences, preventing major disruption to the floral and faunal biomes, and thus, were not the major catalyst driving hominin and faunal evolution as had been postulated. Such dynamic landscapes are not as apparent in southern Africa, which hosts the other major centre of African Plio-Pleistocene hominin evolution (the Cradle of Humankind). By considering the impact of global climate on the 'quieter' southern African region, the role of climate as an evolutionary driver is likely to be more apparent. If inferred palaoevegetation and palaeoenvironmental changes from *Antidorcas* (dietary evidence of prevailing vegetation cover and aridity levels) and/or known hominin adaptation (morphological or behavioural) and *Antidorcas* dental morphology (resulting from adaptive/evolutionary selection pressure) coincide with known global climatic change, climate can be shown to have an influential impact on faunal and hominin evolution.

2.1 Modern environment of South Africa

Today, South Africa is mostly semi-arid with three distinct rainfall zones, and corresponding vegetation biomes (Cowling et al. 2002) partitioning the landscape. Each of these biomes differentially support vegetation utilizing the three main photosynthetic pathways [C_3, C_4 and Crassulacean Acid Metabolism (CAM)] to varying frequencies. The distribution of these pathways is largely determined by environmental factors (Farquhar et al. 1989, see chapter 4).

The winter rainfall zone of western South Africa covers roughly 200km^2, in which roughly 54% of the mean annual precipitation occurs between April and September. The summer rainfall zone is influenced by the warm Agulhas Current that flows along the eastern coast

of South Africa (Lehmann et al. 2016). Between these two major meteorological zones, along the South coast of Africa (southern coast of the Eastern Cape Province into the Western Cape Province), there is a region that receives rainfall during the summer and winter months (e.g. Chase and Meadows 2007). There is the possibility that fossil springbok may have been migrating between the western and southern regions, following the seasonal rainfall and resultant vegetation.

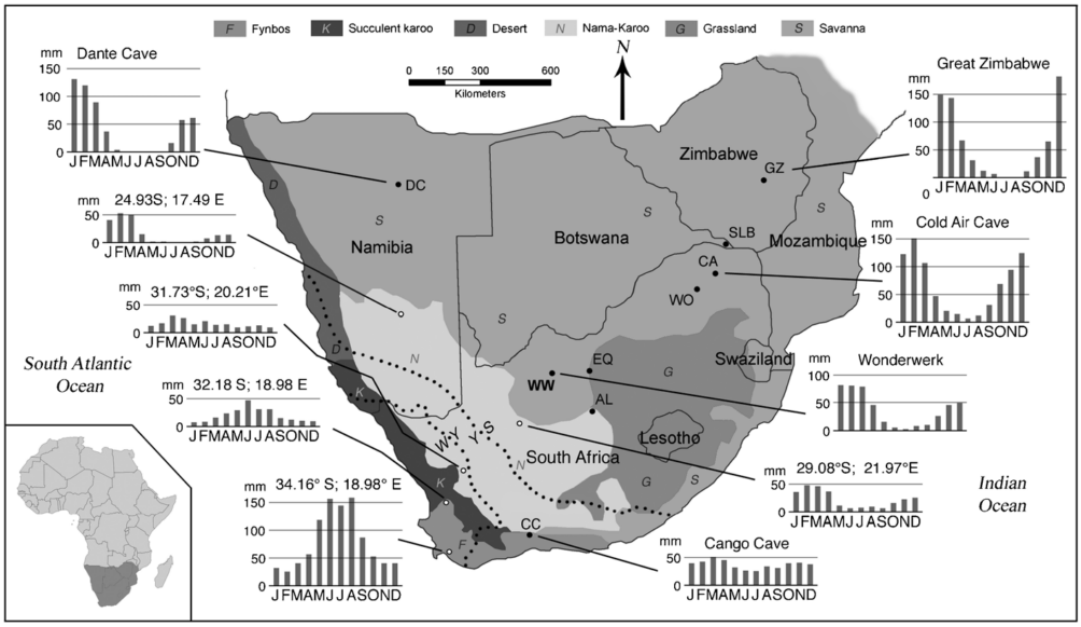


Figure 2.1 Map of southern Africa showing the location of some of the key cave sites (Brook et al. 2015, p.671). The vegetation zones and underlying base map are from Rutherford (1997). The dotted lines are the boundaries between the winter and year-round rainfall zones (W-Y) and between the year-round and summer rainfall zones (Y-S) of Chase and Meadows (2007). The rainfall histograms cover the period from 1961 to 1990 and are from the gridded data of New et al.(1999) as made available at the World Bank's Climate change Knowledge Portal at sdwebx.worldbank.org/climateportal/index.cfm?page=global_map, http://sdwebx.worldbank.org/climateportal/index.cfm?page%25E2%2580%2589=%25E2%2580%2589global_map.

Modern Local Environment of the Cradle of Humankind

Contemporary natural vegetation in the Cradle of humankind is a mixture of open grassland, bush and woodlands (Stuart and Stuart 1997, see Appendices A2). The area is dominated by Rocky Highveld grassland with many natural springs (www.maropeng.co.za). Most rainfall is concentrated in the summer months (650-750mm/year), with temperatures ranging from -12°C to 39°C (www.maropeng.co.za). Modern precipitation is dominated by austral summer rainfall (Tyson et al. 2000). Summer insolation, associated with eccentricity, increases the variability in rainfall (Caley et al. 2018).

2.2 PLIO-PLEISTOCENE PALAEOENVIRONMENT

Maslin and Christensen (2007) suggest there are three main forcing factors significant for regional and global climate change. These are: local tectonics, regional orbital forcing and global climatic changes. A key aim here is to assess the role of climate as an evolutionary

driver for fauna in southern Africa, where local tectonic activity is believed to be less of an influential factor than in East Africa.

East Africa yields more resolute records than currently obtained for South African hominin-bearing locales. The East African landscape is dynamic, with tectonic plates, volcanoes, mountains, greater riverine systems and basins. Although not devoid of dynamic areas, southern Africa's landscape is *relatively* 'quiet' and thus any species inhabiting these areas have fewer evolutionary stimuli. *If*, as hypothesised, climate is a major evolutionary driver, adaptive evolutionary events experienced in southern Africa are more likely to be a response to climate than regional influences more heavily experienced in East Africa (e.g. Reynolds 2007). South Africa contains few deposits that hold a detailed proxy climate record, which has prevented solid links between climate and faunal evolution from being conclusively made. Marine proxies are often cited (e.g. deMenocal 1995, 2004, 2011) but may not be directly transposed to terrestrial settings. One of the few possibilities of obtaining a high temporal resolution terrestrial record is to use evidence contained in speleothems and tufas in the entrance of fossil-bearing caves (e.g. Hopley 2004; Hopley et al 2007b, 2009; Brook et al. 2010, 2015; Sletten et al. 2013; Lehmann et al. 2016). To date, there are currently no terrestrial proxies with an equivalent time span or resolution (to marine proxies) with which to match these records and accurately pinpoint causality.

Figure 2.2 shows the major climatic trends over the past 5 million years (de Menocal 2004, 2011). Climatic changes have been causally linked to increasing aridity and expanding grasslands (Bobe and Eck 2001, Bobe and Behrensmeyer 2002); to evolutionary events (e.g. Brain 1981, de Menocal 1995) and more specifically, these trends have been linked to faunal turnover (Vrba 1985) and hominin evolutionary events (e.g. Vrba 1985; deMenocal 1995, 2011). From the marine oxygen isotope record (deMenocal 1995, 2004, 2011), major climatic 'pulses' occur at ~2.8, 2.4, 2.0, 1.7Ma.

Thus FADs (first appearance datums) and LADS (last appearance datums) in *Antidorcas* species (and other bovid species within the faunal community of the area) may be expected to occur in tandem (during or shortly after, allowing for a lag effect) with these climatic pulses (e.g. Vrba 1985) or be impacted behaviourally (temporary migrations, increased intra-specific variation and dietary variability/change), according to environmental forcing hypotheses (Vrba 1985; Potts 1996, 1998; Maslin and Trauth 2009).

There are numerous ways to investigate palaeoenvironments through a range of proxies (e.g. stable isotope analysis of rock hyrax faecal pellets (Carr et al. 2016), analysis of ostrich egg shell (Ecker et al. 2015) and palynology (Meadows 2015)), some of which are more informative and robust than others. As this is such a vast topic, I will focus on the research directly relevant to the research questions addressed here.

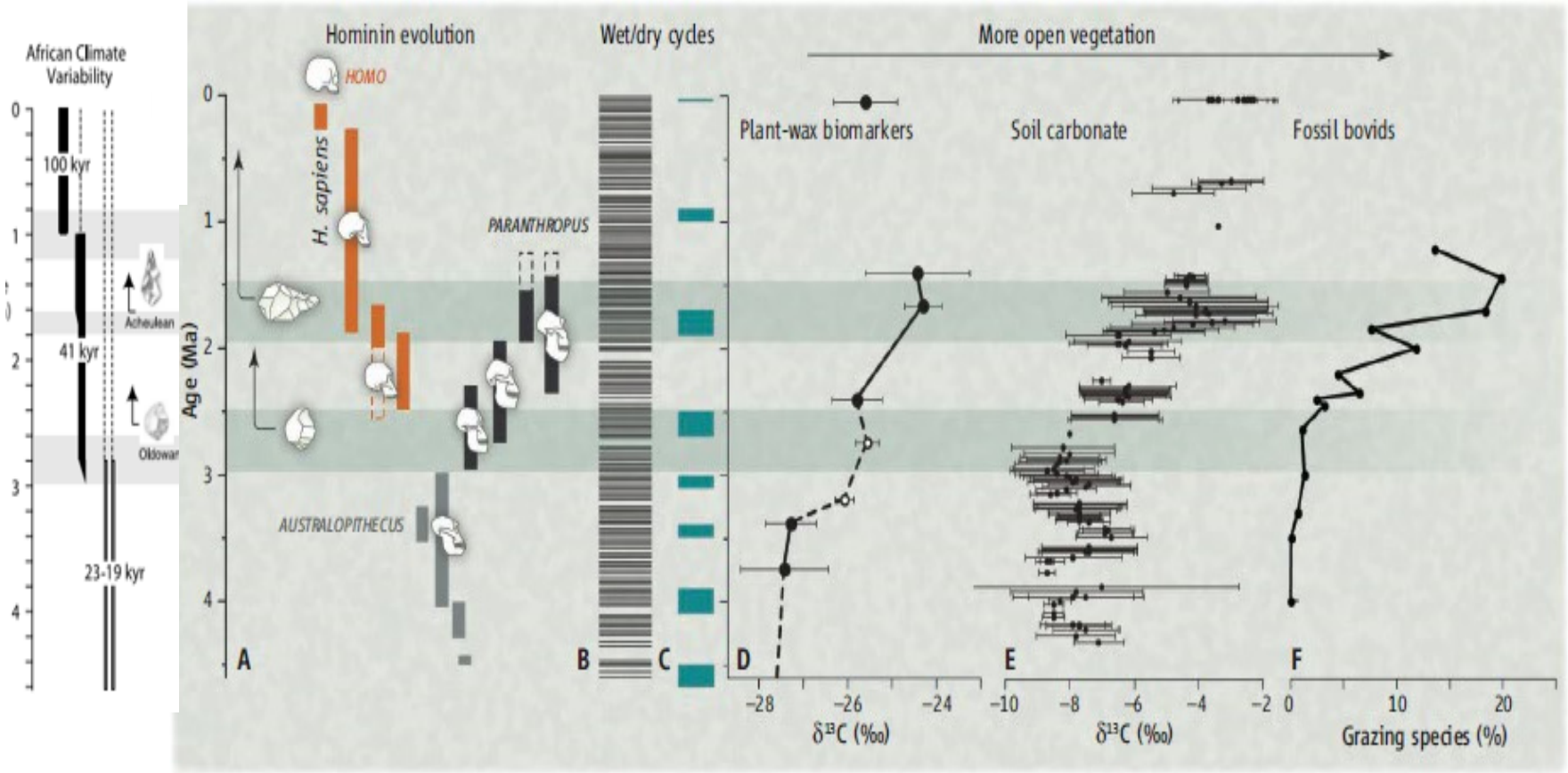


Figure 2.2: Diagrammatic representation of the prevailing concept of climate change relating to human evolution and continental landscape vegetation change, inferred from plant wax biomarkers, soil carbonates and fossil bovid diets (Figure adapted from De Menocal 2004, 2011).

The Pliocene intensification of the Northern Hemisphere Glaciation (iNHG) and African aridification at ~2.8-2.4 Ma has been aligned with bovid and hominin radiation and with the eventual emergence of both *Homo* and *Paranthropus* (Vrba 1988; Vrba 1995; Vrba 1996; DeMenocal 2011). The Pleistocene saw the onset of the Milankovitch (glacial-interglacial) cycles (deMenocal 1995). These ~100,000year climatic oscillations have been causally linked to moderate levels of faunal evolution (Faith and Behrensmeyer 2013). The resultant onset of the Walker Circulation around 1.7 Ma has been associated with the emergence of *Homo* in southern Africa and the appearance of the associated Acheulean toolkit (Vrba 1996; deMenocal 1995, 2011; Hopley et al. 2007).

Furthermore, the aridification and intensified upwelling of the Benguela currents through the Plio-Pleistocene (Lee-Thorp and Beaumont 1995) has been causally associated with the distribution of rainfall zones in southern Africa (Chase and Meadows 2007) and the onset and speciation of the endemic Cape flora (Dupont et al. 2011). Such palaeoenvironmental influences should be visible via herbivore dietary indicators.

2.3 GLOBAL CLIMATE

'Known' global climate is taken from published sources, largely from marine proxies (e.g. deMenocal 1995, 2004). Glacial stages can be visible via increased seasonality and increased precipitations (deMenocal 2004; Mosbrugger et al. 2005). Such colder, drier climatic conditions caused definitive herbivore community structural changes in West Europe, with high turnover peaks during the Middle Pleistocene (e.g. deMenocal 2004; Mosbrugger et al. 2005). Glacial-interglacial cycles of different dominant periodicity (41 Kyr at ca. 2.6 Ma, then 100 Kyr at ca. 1 Ma) have been seen to coincide with seasonal isotope signals (e.g. via European bison sinusoidal variations of seasonal origin over 2.5 years by Bernard et al. 2009).

Proposed major climatic changes:

2.7 Ma: Intensification of Northern Hemisphere Glaciation (iNHG)
2.0-1.7 Ma: Onset of the Walker Circulation (oWC)
1.0 Ma: Mid-Pleistocene Revolution (MPR)

2.3.1 Intensification of the Northern Hemisphere Glaciation (iNHG)

The iNHG is considered to have occurred in the Pliocene (c.5.33-2.6 Ma), between c. 3.6-2.4 Ma (Mudelsee and Raymo 2005), likely c. 2.75 Ma (Haug et al. 2005), as part of a long-term cooling trend (Jakob et al. 2017). The related fluctuations between El-Niño and La-Niña-like climatic states (see glossary of terms) on glacial-interglacial timescales across the intensification of the Northern Hemisphere glaciation, is debated (e.g. Philander and Fedorov 2003; Federov et al. 2006; Bolton et al. 2010; Jakob et al. 2017). The Pleistocene epoch (c. 2.58 Ma) is typified by glacial-interglacial cycles, with the end of the Pleistocene typically seen as the end of the LGM c. 11.7ka (CLIMAP Project Members 1976; Hughes et al. 2013).

During the iNHG, MIS (Marine Isotope Stage) 100 warrants considerable attention, as this is suggested to be the earliest glacial during which the Laurentide Ice Sheet is fully developed (Denison et al. 2005) and advanced into the mid-latitiudes c. 2.5 Ma (Balco and Rovey 2010) with implications for global temperatures and environmental conditions.

Marine records show that there was a shift in climate variability towards more arid conditions after 2.8 Ma, associated with the onset of Northern Hemisphere glacial cycles (deMenocal 1995). Vrba (1985) first causally linked global climate change with African mammalian evolution, citing radiations in bovid species occurring c. 2.5 Ma, which appeared coincident with the iNHG. It is this link that led to the development of the turnover pulse hypothesis (TPH). However, as advancements in palaeoclimatology, mammalian fossil records and ocean drilling programmes occurred, equipped with greater knowledge, the timing and underlying mechanisms of this link and the TPH have been questioned (Maslin et al. 2014). The iNHG began considerably before 2.5 Ma and was a long-term process (Tiedemann et al. 1989) and connections between high latitudes and low to middle latitudes are not as straightforward as originally thought (Maslin et al. 2014). At least for East African sites, it would appear that the iNHG had less of an impact on faunal and hominin evolution (e.g., Behrensmeyer et al., 1997; Faith and Behrensmeyer, 2013) than the subsequent development of Walker Circulation at c. 1.8 Ma (Ravelo et al., 2004).

2.3.2 Onset of the Walker Circulation (oWC)

The development of the Walker Circulation is theorized to have produced the first actual El Niño events in Africa**.** ENSO (El Niño Southern Oscillations) produce extreme climates, typically lasting roughly a year and therefore being influential on the survival of individual animals (i.e. the scale at which selective pressure and evolution works) (Maslin and Christensen 2007). At c. 2 Ma (Ravelo et al. 2004) / 1.9-1.7 Ma (Maslin and Christensen), the onset of the intensified Walker Circulation (deMenocal 2011; Maslin and Christensen 2007) occurred. This saw a re-organisation of tropical climate (Hopley et al. 2007) and marks the start of the 100-year obliquity cycles. The intensified Walker Circulation has been causally linked to mammalian evolution (deMenocal 1995; Vrba 1985). Many studies indicate a shift towards more open landscapes, dominated by C_4 grasses in both south and East Africa (e.g Lee-Thorp et al. 2007, Hopley 2004, Reed 1997). In southern Africa at least, this phenomenon may be linked to the onset of seasonal conditions and vegetation biomes similar to those seen today (e.g. Lee-Thorp et al. 2007).

South Africa becomes much warmer during El Niños, whereas East Africa becomes much wetter (e.g. Wara et al. 2005; Moore et al. 2017). This is when *Antidorcas* might be expected to disperse to southern Africa, during prolonged El Niño events. The contrasting La Niña's produce much colder years. It is this global climatic influence that is arguably the primarily global climate change that has been linked to advances in human evolution (e.g. Hopley et al. 2007; Maslin and Christensen 2007).

Antidorcas might be expected to initiate seasonal mixed feeding as a response to seasonal fluctuations. Modern *Antidorcas* at least, feed according to seasonal conditions, predominantly browsing but shifting to graze after the rains, when fresh grass is in abundance, before grass begins to lignify and becomes unpalatable (Skinner & Louw 1996).

2.3.3 Mid-Pleistocene Revolution (MPR)

The MPR (Berger and Jansen 1994) or MPT (Mid-Pleistocene Transition) (Raymo et al. 1997) is a response to Northern Hemisphere ice sheet increase. From c. 1.0 Ma-0.7 Ma

(MIS 24/23), glacial-interglacial cycles, with a periodicity of 100-kyr, became dominant (Jahn et al. 2003). The glacial-interglacial cyclicity changed from the higher-frequency variations (41-kyr cycles) characteristic of the early Pleistocene, to the lower-frequency variations (100-kyr cycles) characteristic of the late Pleistocene (Jahn et al. 2003). Maximum cooling associated with this occurred slightly later. C. 0.8-0.6 Ma (MIS 17/16) (Jan et al. 2003). At this time, response to obliquity and eccentricity forcing declined, whilst response to precession slightly increased, which is similarly reflected in the dust input and continental climate in South Africa (based on Benguala Current proxy records by Jahn et al. 2003).

Long term trends towards aridification are postulated to coincide with the Mid-Pleistocene Revolution's ice sheet expansion and global sea surface temperature decrease (McClymont et al. 2013). The opposing palaeoenvironmental conditions evidenced for East Africa (wetter, Lake Malawi) and Southeastern Africa (more arid, Limpopo catchment) from c. 1.0 Ma has been suggested to indicate a gradual contraction of tropical rainfall away from Southeast Africa, towards lower latitudes, as a response to the MPR ice sheet expansion (Caley et al. 2018).

2.4 EVOLUTIONARY THEORY

The fossil record is far from perfect with the nature of the material used by no means complete and what is present has been subject to taphonomic processes. Difficulties can arise when using the fossil record to identify species and FADS/LADS (first appearance/last appearance datums) and identifying the timing and nature of evolutionary events. Thus, mechanisms pertaining to evolutionary theory have been postulated, to transpose what is believed about the nature of evolutionary events to what is visible in the fossil record. Speciation, extinction and long-term migrations (dispersion) can be classified as 'evolutionary events'. Environmental / climate forcing hypotheses postulate that global climate is the key evolutionary driver and is necessary for evolutionary events to occur. Following on from the Turnover pulse hypothesis (Vrba 1985), the environmental forcing hypothesis promotes the idea that there is a direct relationship between environmental change and speciation. Although Maxwell et al. (2018) question the reliability of such links without a better understanding of the fossil record and the extent of its accuracy in reflecting the living communities.

In a similar way to which researchers must acknowledge their tendency towards lumping/splitting for species (i.e. if a researcher is prone towards emphasizing the differences being sufficient to warrant branding of a new species, or seeing a range of variation and more conservatively placing similar enough specimens within a single species), the theoretical stance on evolutionary processes taken by the researcher impacts upon their understandings of data and conclusions drawn. Moreover, knowing where to eventually place this research is dependent on the theory of evolution I believe it most strongly fits to. Some of the key evolutionary theories considered here are briefly summarised here. A more extensive overview is given in the appendices (Appendix A1; Table A1.1) and see 'Introduction' chapter hypothesis figure.

2.4.1 Turnover Pulse Hypothesis (TPH)

Vrba's (1985) Turnover pulse hypothesis can be summarised by major biotic turnover (speciation, extinction and dispersion) occurring in pulses, in line with global climatic change (Vrba 1985, 1990, 1993b; Potts and Behrensmeyer 1992). Physical (climate induced habitat / vegetation) change is necessary for the initiation of faunal evolution (Vrba 1993b). These changes, according to this hypothesis, can only occur when environmental changes create fragmentation of habitats leading to vicariance (Potts and Behrensmeyer 1992). Habitat specialists are more likely to be affected by climate and habitat change than generalists (Vrba 1987). In this case, *Antidorcas* (following previous palaeodietary indicators, e.g. Brink and Lee-Thorp 1992; Lee-Thorp et al. 2007) *recki* (browser) and *Antidorcas bondi* (grazer) might be expected to be preferentially targeted by climatic shifts than *Antidorcas marsupialis* (mixed feeder). Turnover pulses may be small, involving only a few species or in a restricted geographic location up to major global events (Bennett 2004).

Vrba's original proposed palaeoclimatic transition, allowing for the assumption of ecological uniformitarianism, was one of a wooded environment around 3 Ma (Makapansgat Limeworks), towards a more open, grassland around 1.4 Ma (Vrba 1975, 1982). Yet the Turnover pulse has limited support in East Africa, where mammalian evolution does not neatly correspond with major ecological changes (Bibi & Kiessling 2015). However, based on recent models aimed to test this theory in vertebrates, the idea of evolution occurring in pulses has re-gained support (Landis and Schraiber 2017). Landis and Schraiber found many vertebrate species were well fitted to Lévy models whereby long periods of evolutionary stasis are intermittently disrupted by pulses of rapid evolutionary change. Crucially though, it has been suggested that apparent 'pulses' in the fossil record reflect only the pulse of preservation (Maxwell et al. 2018) rather than being a reflection of the living community.

2.4.2 Variability Selection Hypothesis (VSH)

Developed by Potts (1996; 1998), the variability selection hypothesis (VSH) proposed that change was not caused by any specific environmental condition or trend but rather by heightened environmental instability. More intraspecific variation occurs as a result of environmental instability and habitat heterogeneity (Potts and Faith 2015). This encourages species plasticity to ensure survival in variable environments. Periods of extreme environmental variability, alternating between wet and dry have been documented for East African Plio-Pleistocene (e.g. Campisano and Feibel 2007; Hopley et al. 2007; Kingston et al. 2007; Lepre et al. 2007; Trauth et al. 2007), which would have a significant impact on the regional climate and vegetation and have been linked to hominin evolution (Potts 1996, 1998). These alternating periods are caused by precession (Deino et al. 2006; Kingston et al. 2007; Maslin and Christensen 2007) creating short periods of rapid, intense forcing followed by relatively weak forcing.

This theory is particularly pertinent to the variable palaeoenvironments around the East African Rift Valley, as a result of their landscape dynamics. For example, variability in the Omo Valley post-2.5 Ma was noted by Bobe et al. (2002). However, Hopley (2004)

suggests that it would be difficult to prove this theory and set it apart from Natural Selection, as well as accusing this theory of being anthropocentric. This theory has subsequently been modified by Maslin and Trauth (2009) and Maslin et al. (2014), to include East African palaeolake activity and is referred to as the 'Pulsed Climate Variability Hypothesis'.

2.4.3 Pulsed Climate Variability Hypothesis (PCVH)

This hypothesis suggests that hominin speciation, dispersals and encephalisation were driven by punctuations in the long-term drying trend in East Africa. Punctuated episodes of short, alternating periods of extreme aridity and humidity leading to climatic variability in 400 or 800kyr cycles driven by the eccentricity maxima (Maslin and Trauth 2009; Maslin et al. 2015).

Maslin et al. (2014, 2015)'s proposed conceptual framework was postulated to examine macro-scale events such as phyletic gradualism and punctuated equilibrium and evolutionary theories at the species level (hominin and *Antidorcas* evolution scale), including allopatric speciation, aridity hypothesis, TPH, VSH, Red Queen hypothesis and sympatric speciation based on sexual selection. It is proposed that each of the differing evolutionary mechanisms hypothesised could have been acting on hominins (and other species) during episodes of climatic instability, resulting in a range of different traits, ultimately leading to the emergence of new species (Maslin et al. 2015). For example, Maslin et al. (2015) demonstrate how the framework can be used to interpret Vrba's (1985) Turnover Pulse Hypothesis and how the TPH scenario would operate under proposed extreme climatic cycles (see Maslin et al. 2015, p.5, fig.5).

2.4.3.1. Smooth model, threshold model, or extreme climate variability model

A 'smooth model' with prolonged periods of wet, followed by long periods of dry environmental conditions, with a smooth transition between each, supports Red Queen or TPH as possible catalysts of evolution. Conversely, a 'threshold model' suggests rapid and extreme environmental variability, in line with Potts' (1998) VSH. The 'extreme climate variability' model is a more extreme version of the threshold model, whereby, extreme climatic variability occurs during transitionary phases between periods of extreme wet and extreme dry environmental conditions.

A fourth possibility posited by Maslin and Christensen (2007) is one of prolonged, extreme wet periods occurring, which could encourage speciation events in a high competition/ high-energy environment that such wet environments promote. This model lends support to the Red Queen hypothesis (Van Valen 1973), as one group succeeds, other co-evolving groups must adapt alongside the successful group, or be outcompeted. However, such prolonged wet environments appear to be limited, at least for East Africa, where this area of research has focused.

Summary of Evolutionary Mechanisms

Substantial progress has been made in recent years, although perhaps only insomuch as adding further factors to consider. For example, the inclusion of individualistic responses within faunal communities, which may be largely temporary but can ultimately confuse the

palaeoecological record (Stewart 2008, 2009; Bennett 2004). However, it is most likely that multiple interacting factors and processes are involved in evolutionary change at all levels. [See Appendices A1].

2.5 PALAEOVEGETATION

Palaeovegetation inferences (*Antidorcas* dietary evidence of use-wear and carbon isotope analysis) and hydrological subtleties (evidenced via *Antidorcas* oxygen isotope analysis) enable suggestions of habitat types present within the landscape and this build a palaeoenvironmental picture for the region (see Appendix A2 for full vegetation and habitat definitions).

There would inevitably be some degree of lag effect expected between climatic changes before this impact is shown through vegetation change and a further period before this vegetation shift is visible through dietary indicators showing *Antidorcas* dietary changes. These dietary shifts could ultimately impact on the *Antidorcas'* dental morphology, again this would be anticipated to be shown considerably later on, after evolutionary adaptation to the changed vegetation. The timings and pace of change would depend on multiple influencing factors.

2.6 REGIONAL PALAEO-CLIMATE AND ENVIRONMENT

Whilst there will be microclimatic and smaller-scale habitat variations, there is a prevailing opinion that southern Africa experienced a gradually increasing aridity (e.g. Bobe and Eck 2001) and spread of grasslands through time after 5 Ma. This has been shown through various methods, such as an increase in grassland-adapted taxa (e.g. Vrba 1973, 1985; Spencer 1997) and isotopic analysis (Hopley et al. 2007; Maslin and Christensen 2007). Interestingly, a second grassland expansion is also shown through isotopic analysis, at 1.75 Ma (Lee-Thorp et al. 2000; Hopley et al. 2007). Around the time which also saw the emergence of the genus, *Homo* in southern Africa. The first appearance of *Homo* in southern Africa is thought to be *Homo habilis* ~1.8 Ma in Sterkfontein Member 4 (Hughes and Tobias 1977) although the taxonomic assignment remains to be confirmed (see Wood and Collard 1999; Pickering et al. 2011).

Recently, basinal-scale habitats (Feibel 1999), local landscape factors (Reynolds et al. 2011), mosaic habitats (Reynolds et al. 2015) or seasonality (e.g. Antón et al. 2014) have been considered to play a greater role than previously assumed in influencing local habitats. The possibility of mosaics habitats challenges the assumptions and bias of previous studies by considering smaller scale factors within the environment.

However, the prevailing paradigm is that southern Africa experienced climate change that saw change from woodland to more open and arid lands from c.2-1.5 Ma. Despite advances from varying methods, a complete picture of palaeoenvironmental reconstruction for southern Africa remains to be achieved.

2.6.1 East Africa

In East Africa, extreme variability intermittently punctuating a long-term drying trend is inferred between 2.8 and 0.8 Ma (Maslin and Christensen 2007). These intermittent

variations coincide with the major global climatic transitions of the intensification of the Northern Hemisphere Glaciation (~2.7-2.5Ma), the intensification of the Walker Circulation (~1.9-1.7 Ma) and the Mid-Pleistocene Revolution (~1-0.7Ma) and this environmental instability has been hypothesized to catalyse hominin evolution (Potts 1996, Maslin & Christensen 2007). However, variations across East Africa exist, for instance, palaeoclimatic records from Lake Malawi show a progressively wetter environmental trend over the past 1.3 Ma (Lyons et al. 2015; Johnson et al. 2016).

Largely due to tectonic faulting, coupled with climatic and environmental interactions and resultant palaeolake availability, East Africa harbours extremely dynamic landscapes (e.g. Bailey et al. 2011; Reynolds et al. 2011). In this environment, micro-habitats can vary dramatically. Because of this, major global climate change can be buffered or exaggerated by dynamic landscapes and unique microclimates in East Africa (Feibel 1999; Bobe et al. 2002; Bailey et al. 2011; Reynolds et al. 2011). The fluctuating presence of palaeolakes for instance can spark variable resource availability and the differential evolution of specialists and generalist depending on lake status (which is in part climatically controlled) (Feibel et al. 1999; Maslin et al. 2014), as water is a fundamental resource for hominins (see Cuthbert et al. 2017) and other fauna. Away from the extreme dynamic landscapes with local environmental buffers encountered in East Africa, South Africa has been seen as a sort of refugium (Reynolds 2007).

2.6.2 Southern Africa

The Cradle of Humankind lies on a fault also, yet the same degree of environmental instability and intermittent palaeolake resource availability (East Africa) as a major buffer for climatic influences is not suggested. Thus, the impact of climate may be more apparent for South Africa than is the case for East Africa. The Plio-Pleistocene expeirenced the onset of glacial-interglacial cycles, with the first major ice-age c. 2.15 Ma (Haug and Tiedermann 1988; Rochling et al. 2014; see section 2.3.2.1). Accordingly, sub-Saharan Africa saw a gradual replacement of woodland habitats in favour of savanna grasslands from 3.0-2.0 Ma (Braga et al. 2016), evidenced by soil carbonate isotope records (Levin et al. 2004; Wynn 2004; Segalen et al. 2007) and deep-sea sediment biomarkers (Feakins et al. 2005).

The East African stable isotope record supports increasing proportions of C_4 plants in the early Pleistocene. In contrast, evidence from stable isotopes, faunal abundance and phytoliths (Bamford et al. 2010) at Wonderwerk Cave (South Africa) show that both C_3 and C_4 grasses and prolonged wetlands remained major components of Early Pleistocene environments in the central interior of southern Africa (Ecker et al. 2018). Climate across the Oldowan-Acheulean transition is driven by global CO_2 levels and regional rainfall seasonality (Ecker et al. 2018), producing regionally distinct vegetation ecosystems for East Africa, the central interior of southern Africa, the coastal regions of southern Africa and eastern southern Africa (Cradle of Humankind).

Hydroclimatic records for the Limpopo catchment area, in which the Cradle of Humankind lies, reveals a long-term trend towards aridification between 1.0-0.6 Ma and marked precessional variability (Caley et al. 2018), the opposite to the trend shown in East Africa

(Lyons et al. 2015; Johnson et al. 2016). Caley et al. (2018) infer this to show an Equatorwards contraction of the rain belt in response to increased high latitude ice volume.

A more humid phase is shown c. 2.0-1.75 Ma, coinciding with the emergence of *Paranthropus robustus* and presence of *Australopithecus sediba*. Consistent with the trend towards drier, more open habitats at Swartkrans (Lee-Thorp et al. 1994, 2000; Sponheimer et al. 2005, 2006; Steininger 2012), the hydrological evidence supports the notion of multi-millennial scale changes and long –term increasing aridity after 1.0 Ma, driven by the MPR. This would see reduced C_3 vegetation, i.e. fewer closed/wooded habitats and reduced humidity (Caley et al. 2018).

2.7 SITES

The geographic area of interest for this research is southern Africa, with the research collection coming from South Africa (Cradle of humankind, UNESCO World Heritage Site, Gauteng province) [25.9254°S, 27.7674°E]. The Cradle of Humankind (CoH) is a series of cave systems with fossil-bearing deposits, predominantly located in the Gauteng province of South Africa (Figure 2.1), with some sites lying outside the geographic area but still referred to as the 'Cradle of Humankind' (such as Makapansgat, Limpopo Province and Cave of Hearths). Specimen lists detailing all collections used are included in the appendices (Appendix A10).

These sites and their stratigraphic unit deposits (members) have been chosen due to their estimated age (Table 2.2) and presence of *Antidorcas* and hominin fossils (or evidence of hominin presence, such as stone/bone tools) within their assemblages. Each member is ordered chronologically (Table 2.2) and used as a proxy for its temporal range. The site members (stratigraphic units) are chronologically combined to provide a relatively continuous temporal range.

This section of the chapter will briefly summarise the sites' stratigraphy, taphonomy and relative chronology (see Appendix A3 for further detail on confounding issues, such as the complexity of cave stratigraphy, relative dating, averaging of assemblages and the nature of deposition, which are addressed for each site individually). The purpose of this chapter is to establish the background to each deposit and highlight, in each case, the factors for consideration when using fossils yielded from them.

Here, when referring to the collective sites within this area of interest, they are referred to as the Cradle of Humankind (CoH), Figure 2.. The CoH spans wider than its strict geographic area to encompass the surrounding hominin bearing localities. The focal sites' assemblages considered for this research are from the Sterkfontein Valley sites (Sterkfontein, Swartkrans and Kromdraai), alongside the younger deposit of the Cave of Hearths, located to the North of the Sterkfontein Valley, in the Limpopo Province of South Africa. The following sites within this locality were used. Their taphonomic processes, dates, formations and other potential confounding factors have been considered prior to using their assemblage material, a summary of which is included in Appendices A3, along with detail of previous palaeoenvironmental reconstructions.

Rationale for using this geographic location

The Cradle of Humankind is one of the key centres of Plio-Pleistocene hominin evolution and have yielded considerable bovid fossils alongside hominin remains (e.g. Vrba 1973, 1974; Brain 1981; Spencer 1997; Avery 2001; Luyt 2001; Steininger 2011). Cave deposition and fossil preservation is not entirely divorced from Plio-Pleistocene climatic changes. Climatic changes could be the cause of deposition and, or preservation. The cave sites are often associated with geological faults (Dirks and Berger 2013), whilst not on the scale of the active faults of East African hominin landscapes; the subtle landscape dynamics played a part in habitat formation, creating favourable environments with key resources (e.g Cutherbert et al. 2017) and fossil preservation (Dirks and Berger 2013). Moreover, CoH cave formations contain the sites from which Vrba initially postulated a causal link between faunal evolution and climate change (Vrba 1985).

Cradle of humankind (South Africa)

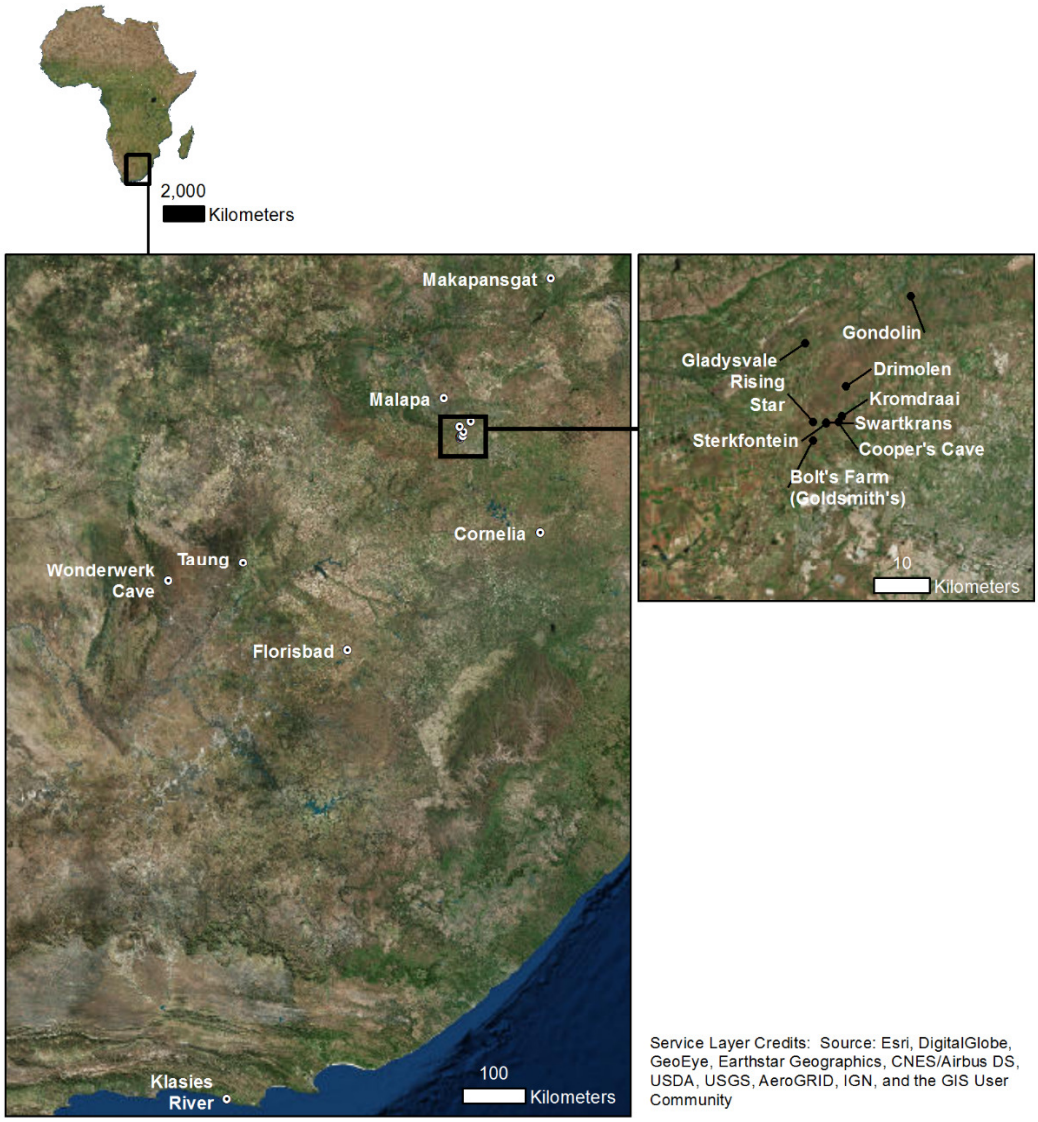


Figure 2.3: A map to show the location of the Cradle of Humankind (top image: within Africa, left: within South Africa) and the main fossil-bearing sites on the right (created by L. Crété).

South African Plio-Pleistocene sites are often subject to dating issues (see Table 2.2), with large date ranges and the lack of agreement between faunal/archaeological dates (e.g. Clarke 2012). The sites rarely yield absolute dates for their deposits. Given the complexities of cave formation processes, it is not surprising that different techniques applied to the same site member may provide conflicting dates (as has been suggested by Pickering and Kramers (2010) and Herries and Shaw (2011) for Sterkfontein). The complexity of the karst deposits lies at the heart of this debate. These deposits result from various processes, each acting on different scales, from large-scale climatic cycles, down to the prevailing conditions at the individual site catchment area. At the very largest scale, climate conditions are linked to planetary orbital variations (Milankovitch cycles) and more regional effects created by circulation patterns and variation in the Earth's surface (de Menocal, 1995; 2004; Hopley et al., 2007). At smaller, local scale, the floral communities are composed of different proportions of C_3 (trees) and C_4 (grass) vegetation, supporting the

fauna associated with these habitat types respectively (e.g. Vrba 1974, 1975; Reed 1997; Andrews and Bamford 2008). Taphonomic processes, (carnivory/scavenging, hydrological conditions and slope wash) control how faunal specimens enter the fossil record, but due to the longevity of deposition, each member is likely subject to multiple taphonomic processes, with several habitat-types possibly represented within a single deposit (Pickering 1999, Hopley and Maslin 2010). Hopley and Maslin (2010) suggest that southern African cave deposits sample more than one processional cycle (~7000 years), and are therefore likely to be 'climate-averaged', with their faunal assemblages showing a mix of species characteristic of both open, grassland-dominated periods of the climate cycle, as well as woodland-dominated extremes (O'Regan and Reynolds 2009; Hopley and Maslin 2010). Moreover, within breccias (fossil-bearing clastic sedimentary rock) there is increasing evidence for cyclic deposition, erosion and re-deposition (de Ruiter 2003; Reynolds et al. 2007; Herries et al. 2009). Any fossil assemblage is only partially representative of the living community due to depositional and taphonomic processes. This is exaggerated in the CoH cave assemblages due to mixing of deposits and may also have implications for, and exacerbate, the dating difficulties posed by these site members. Thus, considerations that interpretations concluding 'habitat heterogeneity' may in fact be a confused mix of distinct palaeoenvironmental periods, from closed and wetter environments to more open, arid ones, masked by time- (and climate-) averaging of deposits (Hopley and Maslin 2010) remains a necessity.

Although the proposed taphonomic processes and accumulating agents for each site member are discussed here (see Appendix A3), Bountalis and Kuhn's (2014) study showed that identifying any *single* accumulating agent or assemblage modifier for cave deposits is highly unlikely. Therefore, each assemblage is utilised with caution and interpretations made only after consideration of these potentially multifaceted processes.

In summary, the complexity of the karst formations affects all other aspects of interpretation, including evidence of climate change, understanding fossil communities, dating possibilities and identifying possible speciation and extinction events (e.g. O'Regan and Reynolds 2009; Hopley and Maslin 2010; Herries et al. 2006; Herries and Shaw 2011). As a result, the evidence for the various patterns observed in the fossil record is best viewed as having been filtered by numerous processes, which should be borne in mind when interpreting data obtained from their assemblages. The sites and their relevant complexities are presented here. These issues do not render the sites irrelevant but simply pose issues that should be considered and mitigated for as far as possible.

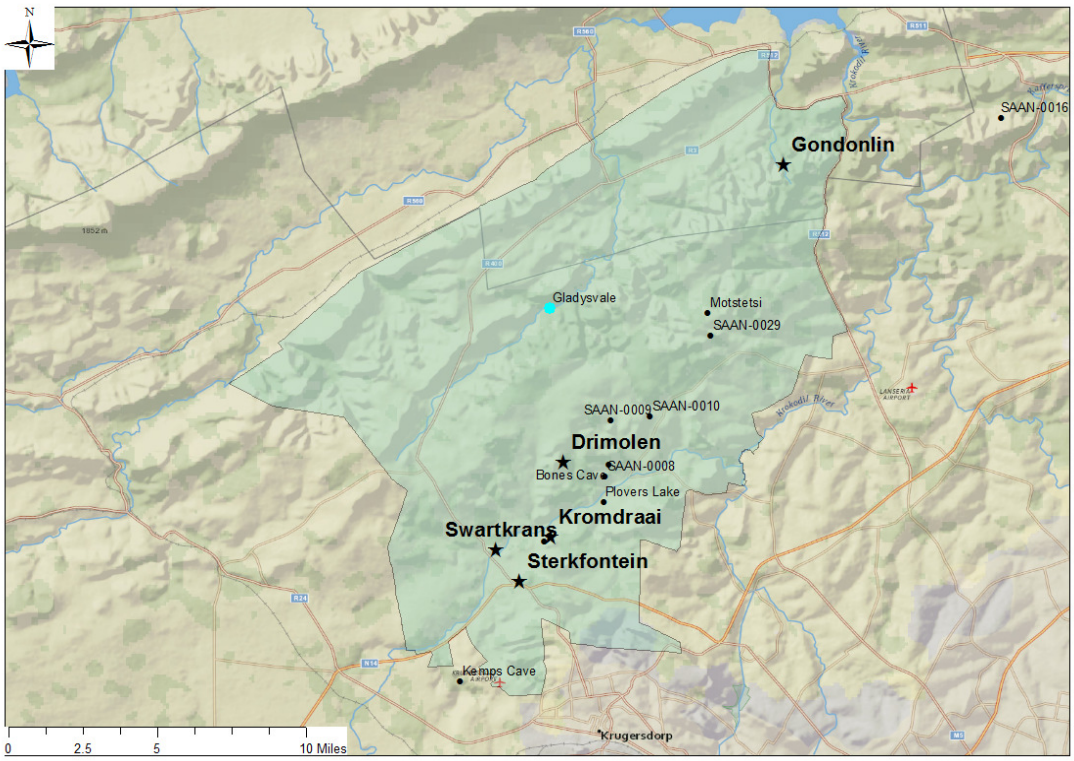


Figure 2.3: Map of the Cradle of Humankind area, with the main hominin site locations indicated.

2.8 IMPACT OF LOCAL FACTORS AND 'MICRO'-HABITATS ON PALAEOVEGETATION AND LANDSCAPE HABITATS

The subtle matrix of small-scale changes in local water, latitude, altitude, geology, topography and soil edaphics can buffer or exaggerate regional climatic influences. The scale here refers to *Antidorcas* / hominin-sized habitats (rather than micromammal/ insect – scale habitats, as may be defined by ecologists).

The Cradle of Humankind

The differential factors influencing the fossil-bearing sites within the Cradle of Humankind area can have bearing on any interpretations made. The impact of the Blaubank river today, can be seen when visiting the area. With closer proximity to the river, Swartkrans' surrounding area is more sheltered, supporting wetter vegetation with more trees, making the area less exposed and arid than the nearby Sterkfontein cave entrance area (Figure 2.4).

Figure 2.4: The surrounding areas of Swartkrans (left) and Sterkfontein (right) to illustrate the 'micro' scale vegetation differences (Photographs taken within a few hours on the same day).

RIVERS: Water bodies, such as rivers, can influence both living communities inhabiting an area, and their subsequent preservation in the fossil record. Water sources, both permanent and temporary, impact upon the habitats supported in the landscape and the taxa within them. The knock-on effects and implications of hydrological changes for the vegetation and canopy cover in an area can have major implications for the fauna inhabiting and depending on these habitats (Feibel 1999). *Antidorcas marsupialis* are water-independent, capable of surviving on very little drinking water when times are scarce (Estes 1991; Skinner and Louw 1996, see chapter 3 '*Antidorcas'*). If the fossil record indicates there are times when *Antidorcas* is more abundant, and this coincides with more water-dependent species being less abundant, this could indicate reduced water availability, i.e. increased aridity (e.g. Ecker et al. 2018). Although, the same water-independence cannot necessarily be assumed for fossil *Antidorcas*, oxygen isotope analysis will provide an indication of moisture (aridity) levels for each member *Antidorcas* dentition is sampled from. The presence of permanent water sources, such as springs and rivers, being used by *Antidorcas* could affect the interpretation of oxygen isotope signals. Differential interpretations of similar results would be either an indication of seasonal rainfall or of *Antidorcas* consuming plants growing around permanent water sources (Lehmann et al. 2016).

A recent model revealed the possible role of groundwater hydro-refugia through orbital-scale climate cycles in East Africa (Cuthbert et al. 2017). Similar may be expected for South Africa. Groundwater can buffer climate variability differentially, supporting habitats according to the respective geology and topography (Cuthbert et al. 2017) and providing

refugia habitats (e.g. Stewart 2008). Hydro-refugia areas in an otherwise arid environment would have been depended upon by many taxa, including hominins (Cuthbert et al. 2017). However, certain water levels are also required for fossilisation to occur and thus there may be an inherent bias in the fossil record towards wetter habitats (Feibel 1999; de Ruiter et al 2008a; Pickering et al. 2007). Even if deposition only occurred episodically, the palaeoenvironmental trends over larger timescales would still be captured. The potential glacial or seasonal fluctuations within that may go relatively unnoticed but comparing each sequential deposit should yield the trend through time (even if just the less arid extent of such).

FIRE can play an important role in shaping vegetation biome distribution (Charles-Dominique et al. 2017; Bond et al. 2002, 2005). For instance, fire can aid in maintaining grassy vegetation, as found in savannas, where climatic conditions may be more suited to supporting woodland and forest-type flora (Bond and Midgley 2012). Fires are typically characteristic of seasonally wet savannas, with the vegetation present being more tolerant to fire (Bond and Midgley 2012).

In the fossil record, it is possible that at some point an aridity threshold was reached that resulted in wildfire, or simply wildfire resulting from lightning strike. In this instance, particularly if these fires were prolonged or rapidly repeated, C_3 plants (larger trees), which are more fire-resistant (Bond and Midgley 2012) would temporarily prevail.

The direct impact of climate-controlled vegetation can be overridden by fire, as it has been in areas of the modern world and throughout history (Bond & Midgley 2017). Brain and Sillent (1988) suggested hominin controlled-fire was evident at Swartkrans Member 3. Beaumont (2011) also infers the presence of repeated burning events to be indicative of controlled fire c. 1.7 Ma. However, fires are likely to have been naturally prevalent within the landscape periodically, causing readjustments within the ecosystem. Evidence of fire presence should be considered when relying on palaeovegetation indicators. Modern *A. marsupialis* consume acacia (*Acacia*) (Skinner and Louw 1996) and may prove an efficient proxy at predicting the occurrence of wildfires in palaeolandscapes, *Acacia* species are known to survive and even flourish from repeated burning. New acacia shoots regrow in the first months of the wet season but photosynthetic rates of the acacia remain high into the dry season months (enabling root starch replenishment) (Schutz et al. 2009).

This is of importance to establish the cause of any apparent palaeovegetation changes; we need to be able to determine whether vegetation changes were primarily influenced by climate or other factors. Fire has been causally linked to major vegetation community changes and consequent megafaunal extinctions (e.g. Gill et al. 2009). Changes in atmospheric CO_2, seasonality of climate and fire are linked to the spread of C_4 grasslands after c. 3 Ma. A consensus remains to be achieved as to the lead catalyst of this expansion but recent models propose that fire is a crucial driver for C_4 dominated biome expansion (Scheiter et al. 2012).

CO2: Major changes in CO_2 levels have been associated with changes in vegetation cover. CO_2 influences plant growth rates, potentially critically influencing the proportions of grasslands to forest within a landscape as well as the tree cover within a savannah (Bond &

Midgley 2017). Low CO_2 levels have been associated with the invasion of C_3 grasslands by C_4 grasses in the Pleistocene (Ehleringer et al. 1997; Scheiter et al. 2012), expanding and contracting the tropical grasslands during glacials and interglacials, respectively (Damsté et al. 2011).

BIOTIC FACTORS: The nature of biotic interactions within an ecosystem is crucial to understanding the influences on faunal turnover and success. Biotic interactions can both drive ecological and evolutionary processes, mediating their ecosystems response to climatic changes, and be themselves driven by the intensity, direction and frequency of climate change (Blois et al. 2013). Whilst care must be taken to avoid uniformitarianism assumptions (Plummer & Bishop 1994), the context of the faunal community in which the *Antidorcas* specimens are found should be considered. A meta-analysis of the faunal communities for each deposit is presented in Chapter 5. Considering the faunal assemblage, places *Antidorcas* in to context of the faunal community, and can provide a contextualized and robust image of habitats available across the landscape.

How *Antidorcas* interacts with other taxa with overlapping niche preferences, such as with the impala (*Aepyceros melampus*) can be indicative of the extent of habitat types and of the degree of habitat heterogeneity. Indirect climate changes (via climate-induced environmental variations) can impact on species interactions, for instance metabolic needs; growth rate changes can alter body size, impacting on species interactions, such as predator-prey relationships, as a result (Vasseur & McCann 2005; Gilman et al. 2010).

INTANGIBLE PALAEOENVIRONMENTAL FACTORS: A factor to consider is the invisible canopy (tree) cover that may actually have been crucial to / dictated *Antidorcas* presence yet remain largely invisible via methodologies available for application to the fossil record. Stapelberg et al. (2008) observed the importance of tree cover to the behaviour of modern springbok (*Antidorcas marsupialis*) in the Kalahari Gemsbok National Park. The presence of trees providing shade as protection against extreme heat or hot winds was shown to be important to the observed springbok behaviour. As the springbok do not necessarily feed on these trees though, their importance for the springbok would not be easily shown in data analysis of dietary signals and dental morphologies. However, we can add to any palaeoenvironmental reconstructions gained from the data in this research, that tree cover is highly likely to have been present within the area also, particularly with higher C_3 plant consumption and / or wetter environments.

Another feature of the landscape utilised by modern springbok but likely difficult to show conclusively via dietary and morphological analyses, is the use of natural licks (geophagy). Kalahari springbok were observed regularly using natural licks in dried river beds (Stapelberg et al. 2008), partly to supplement their diet to fulfil nutrient requirements. This is discussed further in subsequent chapters but has bearing on the palaeoenvironmental habitats capable of supporting certain taxa throughout changeable environments.

One of the crucial issues is in understanding the nature of paleovegetational change. Are changes simply a record of a snapshot in time that happen to reflect different seasons? What is the 'normal' variation for this area and time period and what is the threshold required to initiate environmental change? For accurate interpretation, the fossil assemblage should be

reflective of the living assemblage at the time of deposition. If this is swayed by a particular species for instance, by preferential prey selection or a death trap encountered by a herd of migrating bovids, the disproportionate assemblage would be not be a true reflection of the palaeoenvironment (Vrba 1980). Further, Vrba (1980) states that the autochthonous/allochthonous nature of an assemblage should be known prior to attempting palaeoenvironmental reconstruction. In this instance, this is something we can only speculate on, the *Antidorcas* could have been migrating and thus, be more vulnerable to death. However, comparing the isotopic signatures of the *Antidorcas* sampled with the signals from elsewhere (e.g. other taxa in the assemblage, speleothems, associated breccia) should alleviate this and allow fairly confident assumptions that the assemblages used here represents majority autochthonous individuals.

Cradle of Humankind assemblage formation and cave stratigraphy

The majority of the sites in the Cradle of Humankind are cave deposits and surface finds. The cave deposits harbour complex stratigraphy that are being continuously studied and refined (e.g. Val and Stratford; Stratford et al. 2012, 2014; Stratford 2015). Many of the hominin and faunal assemblages were discovered by mining in the area, when dynamite explosions exposed the fossils.

Cave stratigraphic formation is important for palaeoclimatic reconstruction purposes. The erosional and depositional phases can give insight into the moisture levels and vegetation cover density of the time and by inference, the other climatic conditions (such as temperature) of the time. It has been suggested that cave deposition is highly episodic (e.g. de Ruiter et al. 2008 and Pickering et al. 2007, Pickering et al. 2004, Stratford et al. 2014), with fossil deposition occurring primarily in open, arid conditions (Pickering et al. 2007). If so, the cave assemblages may not be entirely representative of the available habitats spanning this temporal period. These phases are likely to represent glacial-interglacial sequences (Brain 1993a,b,c) or, 'dry/wet' episodes. Sedimentary infill deposition (in which assemblages are preserved) can be highly episodic; with large periods of time likely unrepresented, yet the timing and nature of such episodes are not fully understood (see Pickering et al. 2007). Many of the South African hominin-bearing cave sites are interpreted as reflecting interglacial sedimentation periods and glacial erosion periods (Brain 1995). However, the relatively well-dated site of Gladysvale portrayed the opposite, with flowstones being created during periods of higher precipitation and restricted cave entrances, whereas clastic sediments accumulated during periods with more open vegetation (Pickering et al. 2007).

Maxwell et al. (2018) reported the likelihood that assemblages actually represent a sampling bias, rather than true environmental variation, and only truly indicative of environmental conditions when deposition levels are greater. Therefore, peak taxic diversity reported at 1.9 Ma may be a sampling artefact (Maxwell et al. 2018). Caution is exercised, acknowledging this temporal range has the potential to include more of the living *Antidorcas* assemblage (and consequent variation within) than other deposits used. That is, increased variability for this temporal period cannot automatically be inferred as

'increased', as the preceding temporal range may be underrepresented, with some of the living assemblage absent from the fossil record.

Time and climate-averaging undoubtedly play a part in these assemblages, with some deposits being averaged over thousands of years (Hopley and Maslin 2010) and assemblages can be mixed, combining specimens from across 2 members (mixing specimens over a considerable timespan). This renders population level differentiation extremely unlikely but the member assemblages can be successfully used for comparison against one another to portray a relative trend through time from Sterkfontein Member 4, c. 2.8 Ma to Cave of Hearths < c.0.8 Ma.

This is the nature of cave deposits and is certainly true for South African cave deposits. However, by utilising a species whose remains are more abundant throughout the deposit(s), it is hoped that any trend will be more readily observable, rather than simply yielding a mixed signal.

The assemblages used are detailed in the following chapter (Chapter 4 Materials and Methods) and Appendix A10.

2.9 SUMMARY OF THE PALAEOENVIRONMENTAL RECONSTRUCTIONS TO DATE FOR THE CRADLE OF HUMANKIND

With the considerations discussed in this chapter (and see Appendix A3) borne in mind, the prevailing palaeoenvironmental reconstruction from which to build upon with this research is a transgressive trend with smaller scale shifting habitat heterogeneity. The overall trend shows that Sterkfontein gradually became more open and arid from Member 4 to Member 5 (e.g. Vrba 1974) with this trend continuing throughout Swartkrans Member 1 to M3 (Vrba 1985, Lee-Thorp et al. 2007, see Table 2.1 and detailed more extensively in Appendix A3). These reconstructions however, are still being challenged and adapted in light of new evidence and advancing techniques (e.g. 3D microwear, Merceron et al. 2016; speleothem evidence, Hopley et al. 2007; and hydro-climatology, Caley et al. 2018).

Table 2.1: Summary of Published palaeoenvironmental reconstructions by Member. References[1] Kibii, 2004;[2] Pickering et al., 2004a; [3] Mokokwe, 2016; [4] O'Regan and Reynolds, 2009 [5]Reynolds et al., 2007; [6]Ogola, 2009; [7] Elton 2001, [8]Luyt 2001, [9]Fourvel et al. 2018; [10]deRuiter et al. 2008a; [11]Brophy et al. 2014; [12]Pickering et al. 2007; [13]Avery 2001. Although Kromdraai 'A' and 'B' are now recognised as non-homogeneous, arbitrary prefixes, their published palaeoenvironmental reconstructions are included here to place them into context of the available literature. 'M' stands for Member (cave deposit stratigraphic unit Member). Only reconstructions still considered valid are included.

DEPOSIT	PUBLISHED PALEOENVIRONMENTAL RECONSTRUCTIONS FOR DEPOSITS
	Pre-2.8 Ma
Sterkfontein Jacovec Cavern	A mosaic of both open and closed habitats, comprised of a riverine gallery forest, with bushland and open country[1]. Relatively open with a permanent water supply in the vicinity[2]
Sterkfontein M2	Open grassland and rocky outcrops. [2]Riverine gallery forest with surrounding bushland and occasional open areas with the possibility of standing local source of water.
	2-8-0.5 Ma
Sterkfontein M4	Mosaic habitats with the greatest variety of habitats available[3]. Mosaic but with more dominant woodland component than later Members. Wetter (faunal remains and woody plants- Bamford 1999; Kuman & Clarke 2000). Presence of arboreal primates suggests at least some tree cover[3]. Forest fringe environment with both open and wooded plains[4]. A continuum of forested, open woodland, and grassland habitats[1].
Sterkfontein M5 StW 53 Infill:	Open, drier (than Member 4), grassland.
Sterkfontein M5 East Infill:	Moderately wooded areas[3]. More open grassland than Member 4 but more C_3 vegetation than Member 5 West[8].
Sterkfontein M5 West Infill:	Mosaic but with greater grassland presence than Member 4. Open/woodland grassland or open savannah. A marked shift to drier, more open grassland environments. More grassland than Member 5 East[8].
Sterkfontein Post M6: L/63 Infill	Savannah mosaic environments; savanna woodland and grassland habitats near a permanent water source (such as a swamp or perennial stream)[6]. Changing environment[3]
Lincoln Cave North	Slightly wetter than the earlier Member 5 West and later, Lincoln Cave South and L/63[5].
Lincoln Cave South	Drier, more open grassland environments, similar to Member 5 West[5,6] and modern analogues[5].
Swartkrans M1	Open habitats present[7]
Swartkrans M2	Slightly wetter, more wooded than Member 1 or 3 (e.g. Steininger 2012) Drier than Member 1 with grasslands and wetlands (Bamford 2015).
Swartkrans M3	Mosaic habitat landscapes with a dominance of open grasslands[10,13]

DEPOSIT	PUBLISHED PALEOENVIRONMENTAL RECONSTRUCTIONS FOR DEPOSITS
Plovers Lake	Grassland dominance[10] with similar woodland as today[11]
Gladysvale	C_4 vegetation existed during the early Pleistocene, with a shift towards C_3 dominance during the mid-Pleistocene, but an overall trend of cooler, drier conditions[12]

2.10 DATING

Originally, South African deposits were at the mercy of biochronology and biochronological comparisons with East African sites, which appear to be at discord due perhaps in part to the origination of many species in South Africa, as well as South Africa serving as a refugia for East African populations throughout the Plio-Pleistocene (and therefore not allowing corroboration of appearance datums) (e.g. Lorenzen 2012; Pickford 2004). Fortunately, in recent years, with advancing dating techniques (e.g. Herries et al. 2013; Herries and Adams 2013; Lacruz et al. 2002), biochronology is no longer the leading dating technique for these deposits. The dates used in this study are given in the Table below (Table 2.2). Each deposit is used as a representative of a temporal period, rather than using the material to provide an in-depth analysis on that site per se. All interpretations are subject to change as further temporal resolution of deposits emerge.

*Table 2.2: Dates and methods for each member used. Maximum date ranges are indicated below each Member row. Member deposits ordered chronologically relative to one another (oldest to youngest) based on the dates provided in this table. *The site of Cornelia is not used in this research but is included in this table because of the Kromdraai KA locality comparison of date range based on the Cornelian Faunal span.*

Member	Date	Method	Reference
Sterkfontein Member 4	2.8-2.4 Ma ~2.5 Ma 2.8-2.6 Ma ~2.1 Ma 2.15-2.14 Ma 2.65-2.01 Ma 2.8-~2.0 Ma	Bovid biochronology Primate biochronology Mammalian biochronology ESR (electron spin resonance) Palaeomagnetism Uranium-Pb ESR, and palaeomagnetism	Vrba 1976, 1980 Delson 1984, 1988 Mckee 1993 Schwarcz et al. 1994 Partridge 2005 Pickering and Kramers 2010 Herries and Shaw 2011
Date range: 2.8-2.0 Ma.			
Sterkfontein Stw infill	2.6-2.0 Ma 1.8-1.4 Ma 1.8-1.5 Ma	Biochronology Biostratigraphy ESR and palaeomagnetism	Kuman and Clarke 2000 Herries et al. 2009 Herries and Shaw 2011
Date range: 2.6-1.4 Ma.			
Sterkfontein M5 East	2.0-1.7 Ma 1.4-1.1 Ma 1.4-1.2 Ma	Biochronology and archaeology Dating seriation ESR, isotopes and palaeomagnetism	Kuman and Clarke 2000 Herries et al. 2009 Herries and Shaw 2011
Date range: 2.0-1.1 Ma.			
Sterkfontein M5 West	1.7-1.4 Ma 1.3-0.8 Ma 1.3-1.1 Ma	Biochronology and archaeology Dating seriation ESR and palaeomagnetism	Kuman and Clarke 2000 Herries et al. 2009 Herries and Shaw 2011
Date range: 1.7-0.8 Ma.			
Kromdraai A	1.8-1.6 Ma <1.95 Ma	Biochronology Palaeomagnetism Biochronology*	Pickford 2013 Thackeray et al. 2002

Member	Date	Method	Reference
Cornelian Land Mammal Age	1.07-0.99 Ma	Palaeomagnetism of the Cornelia-Uitzoek type site	Brink et al. 2012
Kromdraai W	2.6-2.3 Ma [Members 1 and 2]	Biochronology	Braga et al. 2017
Kromdraai B	c. 2.6 Ma 2.0-1.77 Ma (c.1.95 Ma) 1.8-1.6 Ma	Biochronology Palaeomagnetism of capping flowstone younger than Member 3 Cited Palaeomagnetism	McKee et al. 1995; Heaton 2006; Pickford 2013 Thackeray et al. 2002 Herries et al. 2009
Date range: 2.6-1.6 Ma			
Swartkrans Member 1 LB	1.8-1.7 Ma	Biostratigraphy	Vrba 1985; Churcher and Watson 1993; Brain 1995, Vrba 2000; de Ruiter 2003a,b
Swartkrans Member 1 HR	1.6 Ma (2.0-1.4) 1.6 Ma	Biostratigraphy ESR	Vrba 1982, 1985; Delson 1984; Brain 1995; Berger et al. 2002; de Ruiter 2003a,b Curnoe et al. 2001
Swartkrans Member 1 (combined)	2.0-1.4 Ma 2.0 (±0.02) Ma	ESR U-Pb bovid enamel dating	Curnoe et al. 2001 Albarède et al. 2006
Date range: 2.0-1.4 Ma.			
Swartkrans Member 2	1.36 (±0.29)Ma (1.65-1.07 Ma) 1.44± 0.05 1.7-1.1 Ma	U-Pb enamel dating U-Pb enamel dating Biochronology Dating seriation	Balter et al. 2008 Albarede et al. 2006 Brain 1995; Vrba 1995a,b: Herries et al. 2009
Date range: 1.7-1.07 Ma.			
Cooper's Cave (D)	1.9-1.6 Ma		Berger et al. 2003
Swartkrans Member 3	0.83(±0.21)Ma (1.04-0.61 Ma) 0.988±0.003	U-Pb enamel dating U-Pb enamel dating	Balter et al. 2008 Albarède et al. 2006

	1.0-0.7 Ma	Biochronology	Brain 1993; Vrba 1995a,b; Herries et al. 2009
Date range: 1.5-0.61 Ma.			
Plovers Lake external deposit	~ 1. Ma	Biochronology	Thackeray & Watson 1994
Plovers Lake	88.7 (±1.36) - 62.9 (±1.3) Ka [0.09-0.06 Ma] 75.6 (±5.6) Ka	U-series dating ESR	De Ruiter et al. 2008a Skinner et al. 2005
Gondolin GD1	1.8-1.7 Ma	Paleomagnetism	Adams et al. 2007, Adams et al. 2016; Herries and Adams 2013.
Gondolin GD2	1.95-1.78 Ma (1.8 / 1.78 Ma)	Paleomagnetism and biochronology	Herries et al. 2006
Gladysvale	~ 0.57 Ma-7ka	U-Th chronology	Pickering et al. 2007
Cave of Hearths	MSA; 0.6-0.4Ma	Biochronology/Radiometric	Wadley & McNabb 2009

CHAPTER 3

ANTIDORCAS: Evolution, Systematics and Palaeoecology, and supplementary species used

A synopsis of the evolution, ecology and other relevant information of the extant *Antidorcas marsupialis* (*A. marsupialis*) and fossil *Antidorcas* (*A. recki*, *A. bondi*, *A. marsupialis* and the potential fourth species, *A. australis*) is presented here. This chapter introduces some of the fundamental aspects impacting upon the modern springbok, which may be used as an analogue to provide a guide as to what *may* be the main influencing factors for the adaptation and evolution of ancestral and extinct species of *Antidorcas*. Literature-based research into the ecology of the springbok is presented in section 1. A synthesis of published fossil *Antidorcas* information is then presented. 'Springbok' refers to the extant species of *Antidorcas*, inclusive of sub-species, 'fossil springbok' refers to all species of *Antidorcas* present in the Plio-Pleistocene, namely *Antidorcas recki*, *Antidorcas bondi*, *Antidorcas marsupialis* and *Antidorcas australis*. Mitigation of influencing factors that could potentially affect interpretations of the fossils is then summarised. The potentially causes of *A. recki* extirpation are then discussed. Finally, a brief ecology of the extant representatives of the fossil species used as supplementary taxa in this research to establish grazing (*Damaliscus pygargus*) and browsing (*Tragelaphus strepsiceros*) parameters, and likely palaeoecology of their fossil counterparts, are summarised in section 2.

SECTION 1: *ANTIDORCAS*

When analysing the fossil record, factors influencing dietary choices should not be overlooked. To anticipate reasonable levels of intraspecific variation in the fossil record, one must understand the variation in the extant community. Therefore, the modern springbok behaviour is considered, in order to understand variations that are likely to have occurred to a similar degree in the past. The extant *Antidorcas* Sundevall (1847), contains a single extant species, with 3 sub-species of *Antidorcas marsupialis* (Zimmerman). The extant species, *A. marsupialis*, is found in southern Africa, south of the Zambezi (Gentry 1966). Fossil *Antidorcas* showed greater diversity however, with 3, or possibly 4, species (the likely presence of a fourth species is discussed in chapters 4 and 6).

Extant *Antidorcas*

Antidorcas marsupialis are herbivorous, seasonal mixed-feeding antelopes, capable of surviving without water for a considerable length of time, obtaining water through feeding on moisture-retaining vegetation, such as succulents (Estes 1999; Kingdon 1997). Though considerably reduced in numbers in recent years, the springbok were previously far-ranging and involved in mass migrations (Dewar et al. 2006; Wilcove 2007). The modern *Antidorcas marsupialis* can be found in South Africa, Angola, Namibia and Botswana. Human influence has led to the considerable decline of springbok populations in recent

years. The fencing introduced across the landscape by farmers, increased human hunting of springbok and the outbreak of diseases such as rinderpest have taken their toll on springbok population numbers. The majority of springbok inhabiting areas south of the Botswana border now live in fenced land (Estes 1991). Their geographic range has contracted and the territories they inhabit may not be entirely representative of their natural preferences. There is some debate about the taxonomic distinction of these geographically distinct populations to sub-species (e.g. Castelló 2016) which is briefly examined but for the purposes of this research, the focus will be on *Antidorcas marsupialis* as a single species. It is perhaps scope for future research to analyse the sub-species within *Antidorcas*.

Fossil *Antidorcas*

As a brief introduction to the proposed fossil *Antidorcas* species, the ancestral *Antidorcas recki* (Schwarz 1932) is found in abundance in both South and East African deposits. *Antidorcas bondi* (Cooke and Wells 1951) is particularly abundant in South African deposits during this temporal range (mainly c. 2.0 – 0.5 Ma); and fossil *Antidorcas marsupialis* (Zimmermann 1780) was also increasingly abundant in South African deposits.

The contentious *Antidorcas australis* (Hendey and Hendey 1968) is found in South Africa and is possibly conspecific or a chronospecies to *A. marsupialis*. The taxonomy of *A. australis* has been disputed*, particularly in the more northern, inland Plio-Pleistocene deposits of the Cradle of Humankind. The taxonomy of specimens identified as '*A. australis*' in relevant deposits is explored in chapter 6.

Figure 3.1: Adult male Antidorcas marsupialis from the Rhino and Lion Nature Reserve, Kromdraai, Krugersdorp, South Africa. [Photograph by L.Sewell, October 2017]. Note the form of the horns.

3.1 *ANTIDORCAS* EVOLUTION

Significant variation in *Antidorcas* horncore morphology, provides the earliest indication of *Antidorcas* splitting from gazelles at least 15 million years ago (Kingdon 1997; Gentry 1966; 2010). The exact evolutionary trajectory of this lineage is not completely understood but it is possible that the modern springbok evolved from forms descended from European populations as some early 'springbuck' fossils are known from Eurasia. Pliocene fossils from the Atlas Mountains show that *Antidorcas* were already adapted to cool Eurasian-type habitats by 4 Ma (Kingdon 1997). Similarly, South west Africa, where modern springbok inhabit is dry and periodically cool (Kingdon 1997). Springbok could have migrated from Eurasia through North Africa and existed in many ancestral forms before thriving in southern Africa. The fossil *Antidorcas* species found in the southern (*A. recki*, *A. bondi* and *A. marsupialis*) and East (*A. recki*) African Plio-Pleistocene are discussed here.

Antidorcas evolution in southern Africa 2.8-0.8ma

Following from *A. recki*'s migration from East Africa, adaptation and speciation events occur in southern Africa. The reasoning behind *A. recki*'s extirpation in East Africa remains unclear and is examined in greater detail later in this chapter. *A. recki* is thought to have migrated to South Africa by c. 2.8 Ma (Sterkfontein Member 4) and the *Antidorcas* lineage

to have evolved further in South Africa. *A. recki* is believed to be ancestral to the modern form (Gentry 1978), splitting into *A. bondi*, and eventually speciating into *A. marsupialis* (or *A. australis* and *A. marsupialis*) (Vrba 1973).

It is believed that many grazers and mixed feeders evolved from browsers as grassland spread (Solounias and Moelleken 1993). This too has been postulated for *Antidorcas*, with the extant mixed-feeding *Antidorcas marsupialis* evolving from the browsing *A. recki* (Vrba 1973). Recently considered for East Africa (Potts and Faith 2015) is the means by which plasticity, mixed-feeding tendencies and highly-specialised behaviour evolves. In southern Africa, a demise in specialised feeders may be expected, alongside an increase in species, such as *Antidorcas marsupialis*, that are more flexible according to on climatic conditions and nutritional availability. With the modern *Antidorcas marsupialis* being highly arid-adapted, this could be indicative of a trend towards increasing aridity, capable of sustaining mixed habitats or, a trend towards aridity alongside variations in environmental stability.

3.2 *ANTIDORCAS* TAXONOMY

3.2.1 Modern Springbok (*Antidorcas marsupialis*)

TAXONOMIC CLASSIFICATION

Kingdom: Animalia
Phylum: Chordata
Class: Mammalia
Order: Artiodactyla
Family: Bovidae
Subfamily: Antilopinae
Tribe: Antilopini
Genus: *Antidorcas* (Sundevall 1847)
Species: *marsupialis* (Zimmermann 1780)

Sub-species

- *Antidorcas marsupialis angolensis.*
- *Antidorcas marsupialis hofmeyri*
- *Antidorcas marsupialis marsupialis*

The single extant *Antidorcas* species, are variable in size at least according to their locality (Skinner and Louw 1996). Understanding the degree of intraspecific variation for modern *Antidorcas* could provide an insight into expected variation in fossil assemblage and allow distinctions between species and sub-species based on variations, and the anticipated thresholds between species and sub-species distinctions for the *Antidorcas* genus. Although generally considered sub-species, these are occasionally elevated to species level (Castelló 2016). Antiquarian sub-species names still present on museum labels (listed below) are now regarded as synonymous with *Antidorcas marsupialis marsupialis (A. m. marsupialis*). *A. m. centralis* (Lyddeker and Blaine 1914), *A. m. euchore* (Sundevall 1947), *A. m. dorsata* (Daudin via Buffon 1802; Desmarest 1804), *A. m. pygargus* (Thurnberg 1811), *A. m. saccata* (Boddaert 1785), *A. m. saliens* (Daudin via Buffon 1802; Desmarest 1804), *A. m. saltens* (Kerr 1792).

Antidorcas marsupialis marsupialis (Zimmermann 1780)

Country Range: South Africa

Range distribution: South Africa, Cape Province, Orange Free State, Transvaal.
Characteristics: The typical springbok. 3 colour variations exist, the tricolour, white and black pelage variations. These colour morphs are sometimes artificially bred on South African farmlands.

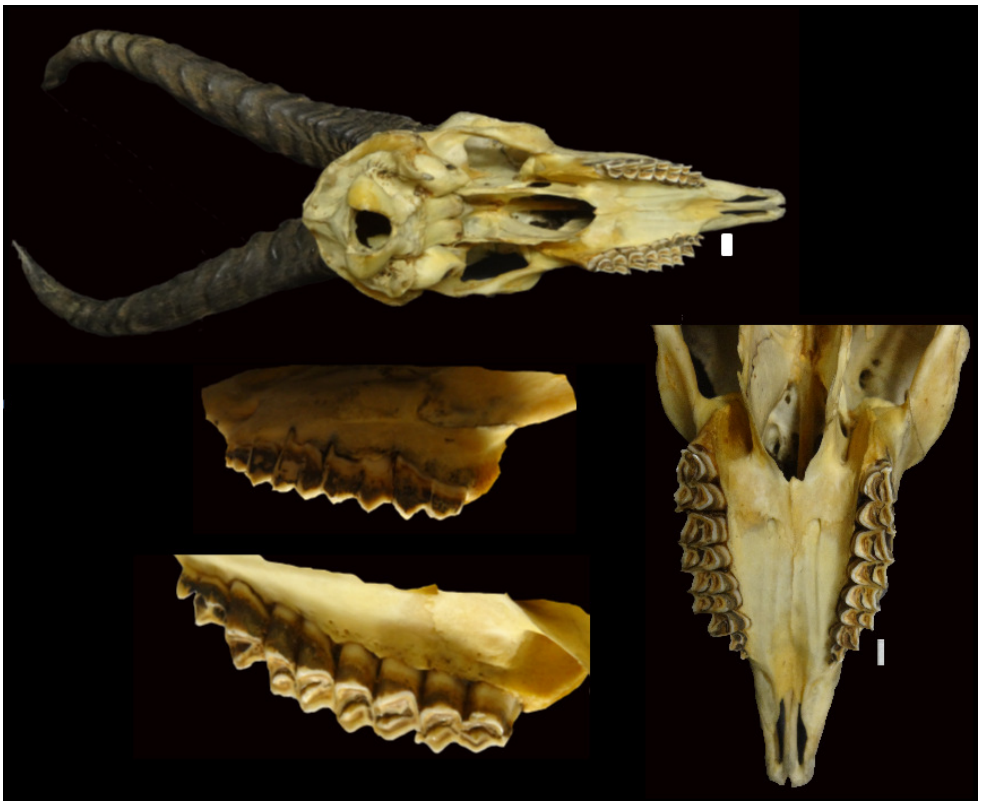


Figure 3.2: Male Antidorcas marsupialis centralis (Lyddeker and Blaine (1914:112)), Type locality is Deelfontein, Cape Colony. Now synonymous with A. m. marsupialis (Cain et al. 2014). Specimen number: NHM.2.12.1.35 (curated at the Natural History Museum, London). Scale bare equals 10mm.

Antidorcas marsupialis angolensis (Blaine 1922)

Country Range: Angola and Namibia
Range distribution: Southwest Angolain Coastal region of Angola, between Benguela and Mossamedes.
Characteristic: Considered slightly larger than the southern populations.

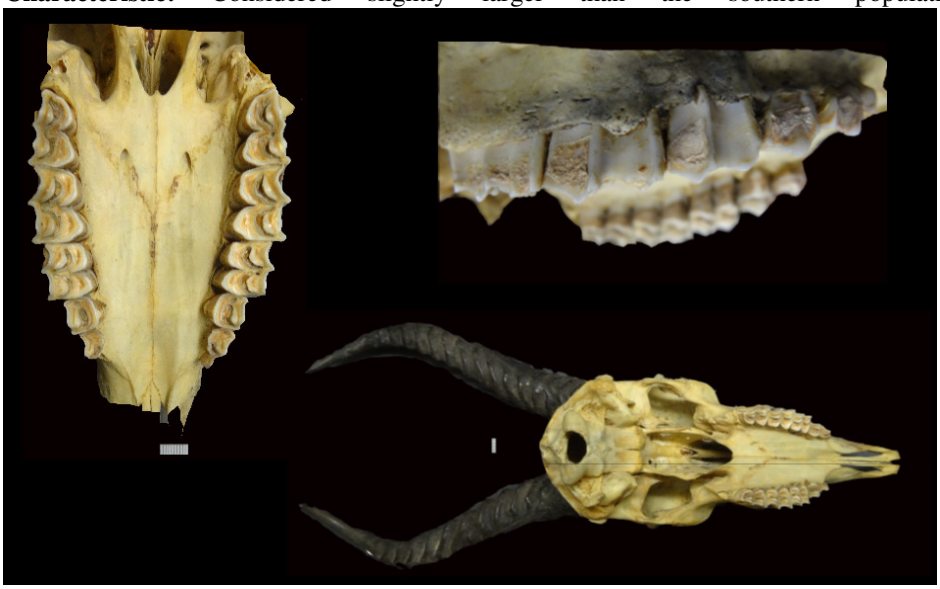


Figure 3.3: Male Antidorcas marsupialis angolensis. Specimen numbers: NHM.20.4.27.32 (curated at the Natural History Museum, London). Scale bare equals 10mm.

Antidorcas marsupialis hofmeyri (Thomas 1926)

Country Range: Botswana, Namibia and South Africa.

Range distribution: Central Namibia to Botswanan Great Namaqualand to the Kalahari and Ngamiland.
Characteristic: Postcranially, this is the largest springbok subspecies. (http://www.planet-mammiferes.org/drupal/en/node/39?indice=Antidorcas+marsupialis+hofmeyri).

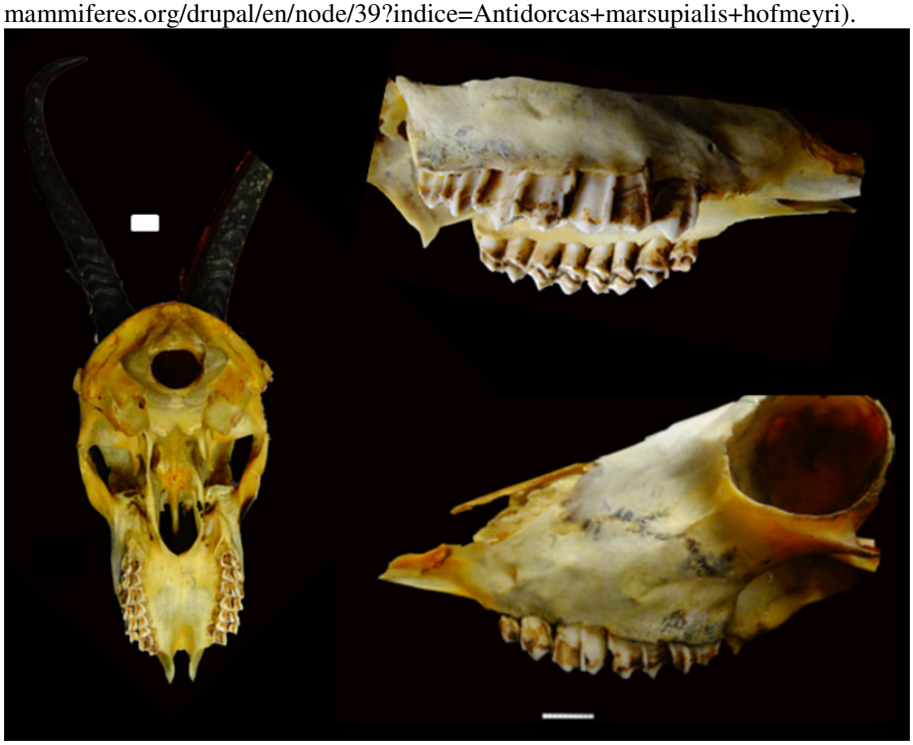


Figure 3.4: Female Antidorcas marsupialis hofmeyri. Specimen number NHM.28.9.11.454 (curated at the Natural Hisotry Museum, London). Scale bare equals 10mm.

3.2.2 Fossil *Antidorcas* Species

Antidorcas recki and *Antidorcas bondi* have been shown to have a similar degree of sexual dimorphism as that displayed by the modern *Antidorcas marsupialis* (Cooke 1996; see chapter 6). Each species is summarised in the following text. Dental traits characteristic of each fossil *Antidorcas* species are summarised more extensively in chapters 4 and 6.

Antidorcas recki (Schwarz 1932)

First appearance (FAD): East Africa, Omo Shungura Member F3 (2.34±0.04 Ma: Feibel et al. 1989). Based on dentition alone, *A. recki* is evidenced to be present in South Africa ca. 3/2.8 Ma-2.0 Ma from Sterkfontein Member 4 but separation from *A. bondi* and *A. marsupialis* can be problematic (Cooke 1949; Vrba 1976, 1995; Turner and Wood 1993; Gentry 2010).

Last appearance (LAD): Difficult to prove due to taxonomic identification complications. *A. recki* disappears from the East African fossil record around 0.8 Ma (Reynolds 2007). The last known appearance of *A. recki* from an archaeological context occurs at Elandsfontein (South Africa) around 0.6 Ma (Vrba 1995; de Ruiter 2003).

Synonyms: Identified as a separate species of the *Phenacotragus* genus, termed '*Adenota recki'* from remains of skull and right horncore at Olduvai OR-NR VIII 343 (Schwarz 1932). Schwarz (1932) assigned *A. recki* to 'Reduncinae,m *Adenota recki'*. This type specimen was destroyed during World War II. Possibly Olduvai's '*Gazella gazelle praecursor'* (Schwarz 1937) also referred to *A. recki* but this was also destroyed during WWII, the same specimen was reassigned to '*Phanacotragus recki'* by Schwarz (1932). Although the type specimen was lost but a cast is held at the Natural History Museum,

London [specimen number M.21460] (Cooke 1996). *A. recki* specimens were referred to thereafter as *Phanacotragus recki* (Schwarz 1932, 1937; Gentry 1966; Leakey 1965) until in 1949, Cooke assigned the specimen to '*Gazella Wellsi'* (Cooke 1949). Subsequently, '*Gazella* sp.' (Leakey 1965, Olduvai), '*Gazella wellsi'* and '*Phanacotragus recki'* specimens were described and likened to the modern springbok but not amalgamated due to lack of definite evidence (Gentry 1966). In 1973, Vrba cited personal communication from Gentry, suggesting *Phanacotragus* and *Gazella wellsi* should in fact be assigned to *Antidorcas* (Reck's springbok) (Cooke 1996; Klein et al. 2007). Vrba (1973) suggested that those specimens previously assigned to *Gazella wellsi* (Cooke 1949) were likely to be conspecific with *Antidorcas bondi* or *Antidorcas recki* (Vrba 1973, p.311) and later, Gentry (1978), encouraged for all *G. wellsi* material to be reassigned to *A. recki,* with the two now being synonymous.

Palaeoecology and distribution: *A. recki* appears to have been one of the most abundant antelope in East Africa and has been recorded from East African sites of Olduvai Gorge, Kanjera, Peninj, Laetoli and Omo (Gentry 1978) and South African sites, in addition to those used in this research, of Bolt's Farm, Elandsfontein and the Vaal River gravels (de Ruiter 2003). *A. recki* has been less well represented in South Africa, and even where it has been recorded, such as by Vrba (1976), the classification of these specimens as *A. recki* has since been questioned (deRuiter 2001). There are fewer specimens assigned to *Antidorcas recki* from either Sterkfontein or Swartkrans. This could be due to issues in differential taxonomic classification, particularly from the descendant *A. marsupialis*, on isolated dentition. This may be further complicated by sexual dimorphism of both species, creating overlap in their dimensions, for example, Adams et al. (2016) report the marked sexual dimorphism apparent for *Antidorcas recki*.

Similar to the modern springbok, the diet of *A. recki* was believed to be browse-dominated (Lee-Thorp et al. 2007). Yet other studies stress the inclusion of grass within a mixed-feeding (mixed grass feeding) diet and a habitat preference of woodland / bushland (e.g. Spencer 1997; Plummer and Bishop 1994). Although similar, *A. recki*'s relative constituents within the 'mixed-feeding' dietary spectrum appear to differ to those of the descendant *A. marsupialis* (Spencer 1997).

Within *A. recki*, there is considerable variation in horncore morphology, which is perhaps indicative of consistent population splitting (Gentry 1978). High levels of feature variation in any species is perhaps indicative of instability and frequent splitting of populations, possibly due to climatic variations.

Antidorcas bondi (Cooke and Wells 1951)

First appearance (FAD): Specimens have been identified as *A. bondi* from Sterkfontein Member 4 (e.g. Luyt 2001; van der Merwe et al. 2003).

Last appearance (LAD): End of the Pleistocene c.7000years ago (Brown & Verhagen 1985; Brink & Lee-Thorp 1992; Vrba 1973; Owen-Smith 1987).

Synonyms: *Gazella bondi,* Bond's springbok. Previously identified as *Gazella bondi* at some sites and subsequently included in '*Antidorcas*' (Gentry 1978). Originally listed by

Cooke and Wells 1951 as '*Antilope* gen. et. sp. indet.', similar dentition was later referred to as '*Gazella bondi'*. Vrba (1973) referring to Gentry's opinion, stated that the '*Gazella bondi'* specimens, more closely fit to *Antidorcas* and should be called '*Antidorcas bondi'*. *A. bondi* has been recorded from Chelmer, Vlakkraal and Florisbad (in addition to the sites used in this research) from South Africa (de Ruiter 2003). De Ruiter (2003) suggests that *A. bondi* is unlikely to fall into the *A. recki* to *A. marsupialis* lineage, yet it is probable that *A. recki* is ancestral to *A. bondi* and *A. marsupialis*.

Palaeoecology and distribution: *A. bondi* has been documented from South African deposits ranging in time from c. 2 Ma (Swartkrans Member 1) (de Rutier 2003; Herries et al. 2009; Pickering et al. 2011) to the Holocene, c. 7Kya (Gentry 2010). *A. bondi* has been suggested to have been the smallest member of a Pleistocene grazing succession (Brink and Lee-Thorp 1992). Stable isotope analysis suggested *A. bondi* was primarily a grazing species around the Cradle of Humankind sites, particularly around its FAD (Brink and Lee-Thorp 1992; Lee-Thorp et al. 2000; Codron et al. 2007) with more mixed–feeding diets from Cornelia (1.07-0.99Ma) (Brink et al. 2012), Florisbad (0.295-0.225 Ma) (Herries 2011) and mixed-feeding to browsing from Haasgat (c. 2.2-2.0 Ma) (Adams et al. 2013). *A. bondi* is the dominant faunal species in Swartkrans Member 2 (de Ruiter 2003; Vrba 1973).

Fossil Antidorcas marsupialis (Zimmermann 1780)

First appearance: The extant springbok, *Antidorcas marsupialis* first appeared in South African deposits in the Cradle of Humankind, at Sterkfontein Member 5 (Vrba 1974) and Swartkrans Member 1 (Watson 1993) c. 2.0-1.4 Ma.

Synonyms: Springbuck. *Antilope marsupialis*, *Cemas marsupialis*. First described by Zimmermann (1780), the fossil *A. marsupialis* is differentiated from *A. recki* by enlarged third molars with larger hypoconulid lobes and longer metatarsals (e.g. Brink 1987; Gentry 2010).

Palaeoecology and distribution: Studies have found the fossil *A. marsupialis* to be a mixed feeder (e.g. Steininger 2012; Lee-Thorp et al. 2007), just like its extant forms and therefore, likely a migratory species. In spite of the large 'trekbokken' of Springbok having ceased in recent years, it is thought that they migrated in large herds at regular intervals (Dewar et al. 2006, Wilcove 2008).

Other sites from the temporal range (e.g. Haasgat c. 2.2-2.0 Ma yielded low $\delta^{13}C$ enamel isotope values Lee-Thorp et al. 2007; Adams et al. 2013.) have found *A. marsupialis*' diet to be broadly consistent with their modern conspecifics with C_3 plant diet-dominance, indicating mixed-feeding to browsing (Gagnon and Chew 2000; Cerling et al. 2003; Sponheimer and Lee-Thorp 2003).

Antidorcas australis (Hendey and Hendey 1968)

Antidorcas australis, described by Hendey and Hendey (1968) was potentially a form smaller than the living springbok, displaying compressed horn cores without a sharp bend backward (Gentry 2010). The taxonomy of *A. australis* as a separate species (i.e. not a chrono- or sub-species, or within the range of variation of *A. marsupialis*) is contentious and warrants further investigation prior to using '*A. australis*' dental specimens for this

research. The specimens assigned to '*A. australis*' (Vrba 1973) are therefore considered separately; see results (Chapter 6, 'taxonomic identification of *Antidorcas* species').

Suggested first appearance date (FAD): Swartkrans Member 1 (Vrba 1973)
Suggested last appearance date (LAD): 11,950± 15014Cyr BP, Nelson Bay Cave (Klein 1983).
Synonyms: southern springbok; *A. marsupialis australis; A. marsupialis/australis*

It is even more challenging than is the case for other fossil species to pinpoint a FAD/LAD for *A. australis* due to taxonomic identification complications. The dentition of *A. australis* is almost identical to that of *A. marsupialis* (Vrba 1973), and the scarcity and fragmentary nature of horncore and/or associated postcranial remains prevents more definitive species identifications. The latest tentatively claimed appearance of *A. australis* would have the last appearance dating to ~60- 50 ka at Die Kelders Cave or as '*A.* cf. *australis'* (Klein, 1980, 1983) (11,950± 150 14C yrs BP= 13,430 to 14,140 cal yrs BP) at Nelson Bay Cave (Schwarcz & Rink 2000; Klein & Cruz-Uribe 2000; Feathers and Bush 1999). Alternative suggestions of the End of the Pleistocene (12,000-9,000BP; Owen-Smith 1987) and similarly, the late Pleistocene-Holocene transition (Faith 2014) have been suggested for the last appearance of *A. australis* forms.

Palaeoecology: *A. australis* is associated with open habitats, alongside grazers such as Equids (Faith 2014) but believed to be a mixed feeder (Klein 1980). However, Lee-Thorp et al. (2000)'s carbon isotope study shows '*Antidorcas australis'* to be a predominantly browsing herbivore.

Antidorcas australis identification history: Hendey & Hendey (1968) described *Antidorcas marsupialis australis* as a new sub-species of springbok from Swartklip, near Cape Town (Brain 1993). When Vrba (1973) discovered similar fossils from Swartkrans, this 'sub-species' appeared more widely distributed and thus was deemed to warrant distinct species status. From this, *A. recki* was assigned to being ancestral to *A. bondi* and then at a later stage, ancestral to both *A. australis* and *A. marsupialis*. Vrba (1976) since disputed this, preferring to refer to the Swartkrans material as 'pre-*marsupialis*', representing an evolutionary transition between *A. recki* and *A. marsupialis* (see Figure 3.6). Some years later, many of Vrba's original classifications of *A. australis* were reassigned e.g. to *A. bondi* by de Ruiter (2003).

Cooke (1996) states that *Antidorcas australis* is a southern species, not found in northern breccia (rock typical of the Cradle of Humankind cave range in which fossilised remains are typically found) sites. However, it is not easily differentially identified from *Antidorcas marsupialis*, certainly not from dentition alone. Therefore, caution is suggested before ruling out its presence/absence from any sites from its believed temporal range. There are numerous examples of re-identification of taxonomic assignment for various faunal remains. Cooke (1996) suggests the possibility of *Antidorcas australis* material perhaps being actually *Antidorcas recki*. Despite dental similarities, identification difficulties should not necessarily dictate the lumping of species as it is a known phenomenon within modern zooarchaeology that sheep and goat are extremely difficult to tell apart, even by experts in the field (e.g. Zeder and Pilaar 2010). When translated to fossilized species, the problem is undoubtedly exacerbated without any historical documents or known ecologies to rely on to

aid differentiation. Some confusion may arise when attempting comparisons with published data when the same specimen has been assigned to an alternative species.

The legitimacy (and accuracy of its identification in Cradle of Humankind contexts) and palaeoecology of this proposed taxa is yet to be untangled and is one of the key focus' of this research as a part of the aim of understanding the palaeoecology of the *Antidorcas* lineage.

Characteristic features for *Antidorcas australis* identification: The differential lyrateness of the horns of *A. australis* (Hendey and Hendey 1968) compared to other fossil springbok, may differentiate more readily from other *Antidorcas* forms, enabling easier identification than is possible from dentition alone. Unfortunately, horncores are rarely found intact with dentition on *Antidorcas* crania within these deposits from which to conduct a detailed study. Based on dentition (see Figure 3.5), *A. australis* specimens have only been tentatively identified (e.g. Vrba 1973) due to being slightly narrower than those of *A. marsupialis*.

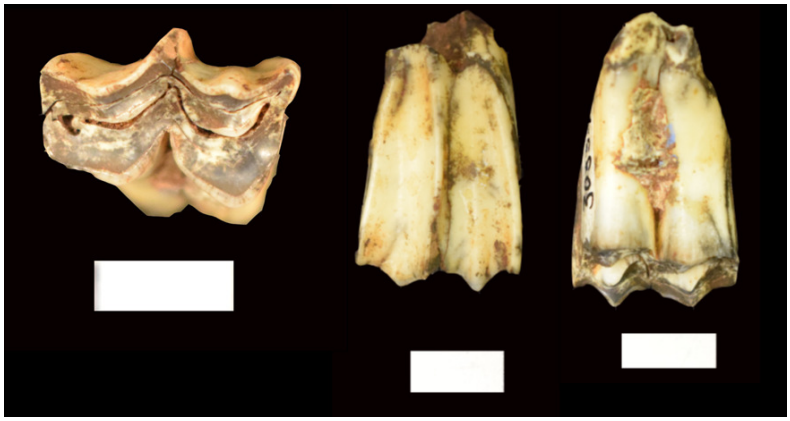


Figure 3.5: An example of potential Antidorcas australis maxillary dentition, SKX 30334 Swartkrans Member 3, RM² (identified as 'A. australis' by Vrba 1973). From left to right: occlusal, buccal and lingual views. Scale bar represents 10mm. Original photographs taken by L. Créte 2017.

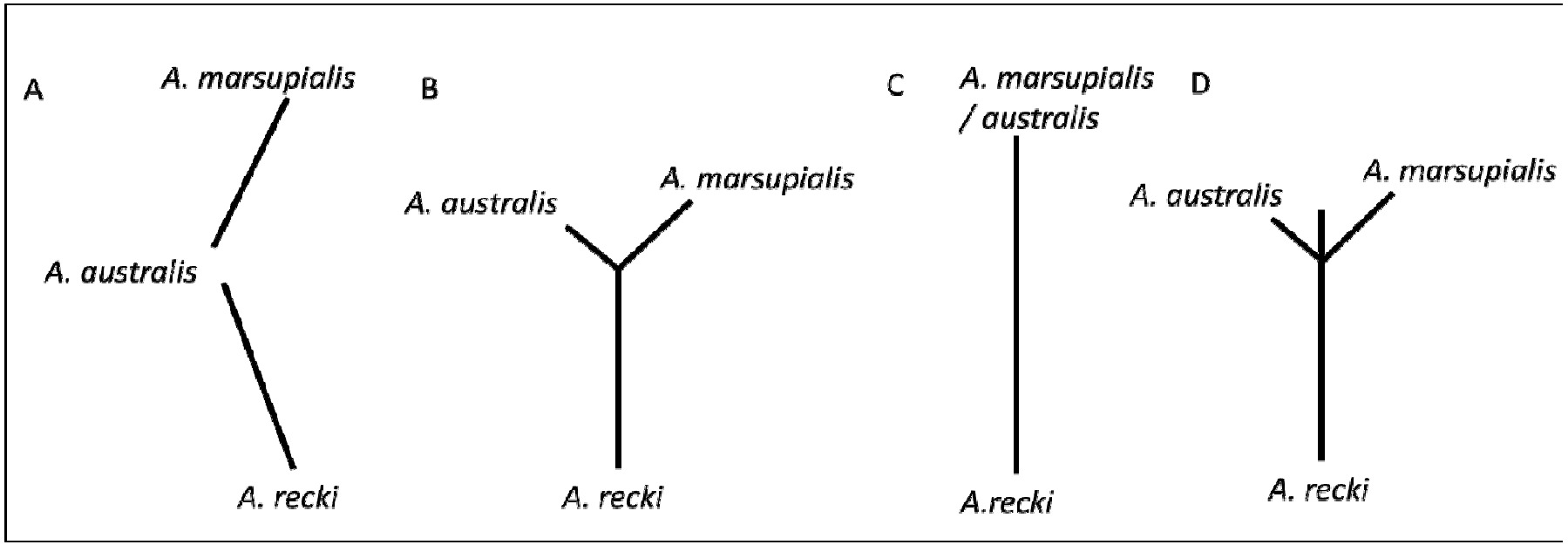


Figure 3.6: Possible evolutionary scenarios for Antidorcas australis.; A: A. australis is a transitional form between the ancestral A. recki and the descendant A. marsupialis; B: A. australis and A. marsupialis are separate species, both descendant from A. recki; C: There is no species distinction between A. australis and A. marsupialis but A. australis could be a sub-species of A. marsupialis, both descendant from A. recki; D A. recki splits into A. marsupialis (and potentially a branch to A. australis additionally) as a sister species but temporarily continues to exist as a species alongside.

3.3 *ANTIDORCAS* ECOLOGY AND PALAEOECOLOGY

Extant *Antidorcas* Ecology

"Springbok are both selective and opportunistic feeders that adjust their diet, microhabitat and foraging time to the highly variable quality of the forage in arid areas. In doing so they can change from habitat generalists and diet specialists to habitat specialists and diet generalists, depending on environmental conditions. They do, however, remain selective foragers at all times and avoid highly lignified forage plants."
(Skinner & Louw 1996, p. 24).

Distribution

A. marsupialis are found in South Africa, Namibia, Botswana and Angola. The relative distribution of springbok sub-species tends to be geographically isolated. The current distribution of springbok population (

Figure 3.7), has been blighted by diseases (e.g. rhinderpest) and human intervention (hunting and farming enclosures, restricting their habitat availability and movement). The majority of springbok south of the Botswana border now live in fenced land (Estes 1991; Skinner and Louw 1996). Springbok typically inhabit savannas or grasslands, where vegetation is short (low and fresh grass and shrubs), often associated with the edges of dry river/lake beds (Bigalke 1972; Milton et al. 1992; Skinner and Smithers 1990), to promote vigilance and movement, as an anti-predator response (Bigalke 1972; Smithers 1983). Although capable of inhabiting many biomes, *A. marsupialis* does not inhabit mountains or woodland with tall, dense vegetation (Estes 1991).

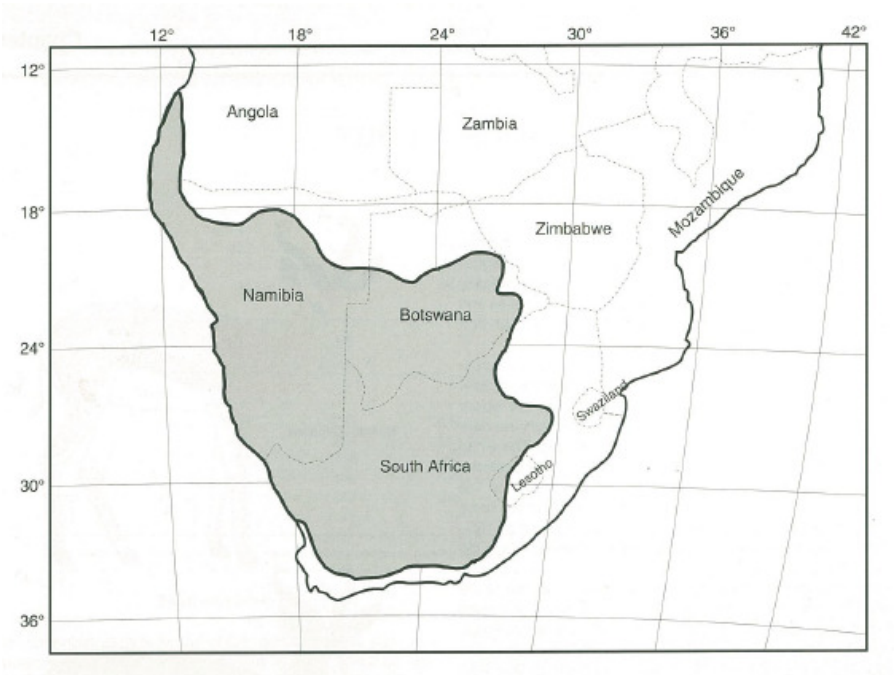


Figure 3.7: A map of current Springbok (Antidorcas marsupialis) distribution (Skinner and Louw 1996, P.9).

Behaviour

Springbok behaviour has been reported to vary seasonally (e.g. Kingdon 1997), according to multiple factors, as will be discussed in the following sub-sections. The implications of such seasonal variation, when extrapolating back to fossil springbok for palaeoenvironmental reconstruction purposes, are cause for consideration (as will be discussed).

DIET: Although categorized as a mixed feeder, the springbok has been observed to be primarily a summer grazer and a winter browser (Kingdon 1997; Skinner and Louw 1996; Gagnon & Chew 2000), overall having a browse-dominated dietary pattern, feeding on karroid, dicotyledonous vegetation particularly in the cold, dry season but grazing largely in the hot, rainy season, where grass shoots, especially favouring young succulent grasses before they lignify (East 1999; Skinner and Chimimba 2005; Bigalke 1972; Van Zyl 1965; Estes 1991; 2017). This is largely in response to grass availability. The springbok can survive on very little water (Estes 1991; Kingdon 1997; Skinner and Louw 1996) and tolerates water with a high mineral content and often obtains water from succulents and the food it eats but will drink water when it is readily available (Nagy and Knight 1994).

Springbok have been observed feeding on karooid vegetation from riverbeds and dry lake beds as well as foraging on tall shrubs or consuming leaves from the ground and occasionally will dig for roots (Bigalke 1972; Eloff 1959; Van Zyl 1965; Cain et al. 2004) or seek succulents and cucurbits (gourds) in the absence of surface water (Kindon 1997). Some of the favoured vegetation are succulent shrub leaves (e.g. *Acacia mellifera*) and coarse/hard-stemmed grasses, including *Aristida*, *Eragrostis*, *Cynodon, Panicum* and *Sporobolus* (Davies et al. 1986; Nagy and Knight 1994; Skinner 1996; Skinner and Louw 1996).

Table 3.1: Diets of male springbok during observation in the Kalahari from stomach contents. Table adapted from Nagy & Knight 1994 pp. 866-867.

Season		Plant species	Part of plant	Percentage of diet (%)	Energy content (Kj/g dry mass)	Water content (ml H^2O/g dry matter)
Hot, dry	With drinking water	*Stipagrostis obtusa*	Dry leaves	65.1	16.5	0.064
			Green leaves	10.3	18.2	1.950
		Rhigozum trichotomum	Green fruits	5.9	17.7	4.977
			Small twigs	5.5	17.3	0.377
			Dry flowers	1.6	17.6	0.092
		Acacia erioloba	Dry seed, pod	5.5	18.0	0.054
			Leaves, flower stems	0.7	18.5	0.556
		Acacia mellifera	Old leaves	0.9	18.7	0.556
		Boscia albitrunca	Green leaves	0.8	14.3	2.532
		Monechma incanum	Flowers	0.7	17.1	0.100
		Gisekia africana	Green leaves	1.7	16.3	5.745
		Unknown		1.3		
		Weighted mean			**16.9**	**0.699**
Hot, dry	Without drinking water	*Acacia mellifora* and *A.hebeclada*	Flowers	15.9	18.9	1.559
			Leaves	0.3	18.3	1.062
		Acacia erioloba	Seeds	10.6	17.8	0.022
			Leaves	1.0	18.8	1.385
		Stipagrostis	Dry leaves	9.0	15.8	0.014

		obtusa	Green leaves	0.5	18.7	0.775
		Boscia albitrunca	Leaves	1.4	18.6	1.006
		Unknown	Flower pulp	61.1	18.9	1.559
		Weighted mean			**18.5**	**1.241**
Hot, wet	With drinking water	*Stipagrostis obtusa*	Green leaves	15.7	17.5	1.008
			Old leaves	52.0	16.3	0.445
			Dry leaves	13.8	17.2	0.171
		Acacia mellifera	Green leaves	5.0	19.5	0.980
		Rhigozum trichotomum	Green leaves	4.9	17.5	0.786
		Acacia erioloba	Green leaves	1.8	19.5	0.923
		Tribulus terrestris	Stems	6.8	17.4	0.296
		Weighted mean			**17.0**	**0.537**
Cold, dry	With drinking water	*Stipagrostis obtusa*	Leaves, stems	14.3	18.0	0.120
		Acacia mellifera	Old leaves	41.8	18.6	1.062
			Dry leaves	1.8	20.2	0.042
		Monechma incanum	Dry leaves, stems	4.8	16.6	0.514
		Tribulus terrestris	Stems	5.1	15.1	0.028
		Acacia erioloba	Old leaves	2.2	20.7	0.851
		Boscia albitrunca	Green leaves	5.1	119.2	0.870
		Unknown	Leaf pulp	24.8	18.6	1.062
		Weighted mean			**18.3**	**0.814**

Interestingly, from the observations of springbok in the Kalahari by Nagy & Knight (1994), the springbok ate a wider range of foods with relatively high water content in the hot, dry season without drinking water but chose fewer, higher water-rich plants (and plant parts) in the hot, dry season with access to drinking water. The latter choice provided comparatively less energy to the springbok than plants with lower water content (as may be expected). The overall mean water consumed was higher from utilising the range of plants with relatively lower moisture content, which also provided comparatively more energy than the plants with higher moisture content. In accordance with many similar-sized antelopes, springbok feed most intensively around dawn and dusk (Kingdon 1997), when moisture content of vegetation is high. Without access to drinking water, the springbok consumed predominantly flowers, whereas with drinking water available, their highest intake was from the leaves (from various plant species) with *Stipagrostis obtusa* being an apparent preferred species. *Stipagrostis obtusa* is a species of perennial grass (monocot), requiring relatively large quantities to fulfil nutritional requirements, hence why larger quantities of this species may be consumed.

This may prove relevant for stable isotope analysis interpretations (see chapter 10). Whilst Table 3.1 is a snap-shot into the dietary habits of male springbok, these observations could

be useful in interpreting some of the dietary indicators from fossil *Antidorcas.* For instance, the preferred plants could highlight the cause of microwear scarring seen on dental enamel surfaces (see chapter 4, for explanation of DMTA variables). As an example, the expected dietary use-wear signal from *Stipagrostis obtusa* would be one of high enamel wear anisotropy, low complexity and low heterogeneity (microwear), i.e. a summer grazing signal. However, it is likely that this vegetation species was consumed alongside other vegetation (seasonally and alongside other summer grazing vegetation types), more likely to produce wear typical of abrasive mixed feeding (high relief with rounded cusps mesowear signal; medium anisotropy, medium complexity and high heterogeneity microwear signal). The impact upon microwear values of consuming succulents, cucurbits and roots would presumably create a similar range to that of fruit-browsing/mixed-feeding. There is the potential to understand seasonality from corroborations with this type of modern observational data also, with comparisons of the fossil observations (via carbon/oxygen isotopes or microwear signals) with the plant species, plant parts and their respective nutritional (energy and water content) properties.

Kalahari springbok have also been observed to make use of natural 'licks', presumably to supplement their diet (Stapelberg et al. 2008). When and where any natural lick areas would have been present and utilised in the Plio-Pleistocene is not known.

Fossil Intangible traits and behaviour

Extinct *Antidorcas* species would have had intangible traits that although not directly visible, could have allowed survival in certain habitats or encourage dietary changes. For example, their pelage (properties of their coat-including colour and thickness) may have contributed to their demise should other species occupying a similar niche thermoregulate more effectively in fluctuating climates. Optimal feeding, reproductive behaviours and vigilance would be vulnerable to compromise. Thus, the springbok would be outcompeted. We might expect to see this for example, in variable climates or major climatic shifts around 2.8, 1.7 and 1.0 Ma (e.g. deMenocal 1995), exaggerated if species such as impala are present or if multiple *Antidorcas* species co-exist at any one time. Although largely intangible, their effects could impact the data obtainable, those that may directly impact data obtained in this research are discussed briefly here (see Appendices A5 for further discussion).

THERMOREGULATION**:** Modern springbok adjust their behaviour throughout the day as a response to thermoregulatory needs compromised with nutritional requirements (Skinner and Louw 1996). Springbok have a thin pelage, leaving it vulnerable to extreme temperatures. Where feeding requirements mean feeding in sub-optimal sun intensity or temperature conditions, the animal either seeks shade or orients its body accordingly (Skinner and Louw 1996). The pelage and thermoregulatory needs and responsive behaviour to variable climates of extinct *Antidorcas* are unknown. The speculative possibility exists that fossil *Antidorcas* species died out due to increased aridity and reduced shade as grasslands expanded and tree cover reduced. This could be loosely inferred via dietary vegetation proxies and oxygen isotope ($\delta^{18}O$) values could be used as supportive evidence for thermoregulation-implicating hypotheses.

Figure 3.8: Springbok (Antidorcas marsupialis) observed at the Rhino and Lion Nature Reserve within the Cradle of Humankind World Heritage Site, Gauteng Province, South Africa.

Herd demographics

Figure 3.9: Springbok (Antidorcas marsupialis) observed at the Rhino and Lion Nature Reserve within the Cradle of Humankind World Heritage Site, Gauteng Province, South Africa.

Herd demographics and Male / female springbok behaviour can differ seasonally, such as during the rutting or lambing season, with their nutritional needs fluctuating differentially throughout the year (more dispersed in the dry season). Dietary differences can also be dimorphic as a result of herd demographics and differential habitat preference, vigilance requirements and many other related factors. Modern *A. marsupialis* of known sex can be used to inform on the predicted degree of sexual dimorphism likely in the fossil record. Although this can only be based on assumptions on the behavioural similarity of fossil species, it can nonetheless be used as a helpful indication. The social constraints, such as individual ranks, age and sex within herds may impact on food selection (Appleby 1980; Côté 2000). This factor should be borne in mind when interpreting dietary indicators, particularly of fossil *Antidorcas*.

Sexual Dimorphism: Different selection pressures act on males and females throughout the year. This factor is worth bearing in mind when considering the success of the lineage in contrast to others. For example, nutritional requirements of the female can fluctuate according to season and reproductive status. The quality and quantity of the available vegetation can dictate the success of the springbok ewe and her lamb(s). Modern springbok data will be tested for sexual dimorphism as a factor, to ensure any similar patterns in the fossil data are not misinterpreted as signifying distinction of species.

Although lambing can happen any time of year, it tends to peak in summer within the summer rainfall period, with the breeding process correlated to the onset of the spring rains (Skinner and Louw 1996; David 1978).

Migration: Until the end of the nineteenth century, huge migratory herds of springbok were witnessed (Wilcove 2007, Estes 1991, Kingdon 1999, Dewar et al. 2006). Referred to as 'trekbokken' (Bigalke 1972, p. 338), large numbers of springbok would come together from the interior of the Kalahari and Karroo and invade surrounding areas during times of drought when the animals were essentially forced outside their normal range (Estes 1991). Bigalke (1972) reports on this trend being observed following a period of unfavourable conditions in the favoured habitat of the springbok. The level of migration, seasonal or

otherwise, in extinct *Antidorcas,* is unknown. That *Antidorcas marsupialis* was previously known to embark on periodic mass migrations (Dewar et al. 2006; Berger et al. 2006) suggests the migratory tendency may have been prevalent in the ancestral form.

It is possible that the palaeovegetation signal obtained here will reflect a larger regional scale, if the extinct forms migrated on a similar scale to the extant springbok. Thus, although assemblage provenance is used as a means to show temporal range, *Antidorcas* data cannot definitively give a vegetation reconstruction on the microscale for each site. Vrba (1980) states that the autochthonous or allochthonous (indigenous/immigrant species) nature of an assemblage should be known prior to attempting palaeoenvironmental reconstruction. Modern springbok are thought to follow their preferred vegetation according to the seasonal climate (Bigalke 1972). Should their preferred vegetation have been lacking around the Cradle of Humankind at any point, perhaps seasonally, the springbok species *could* have migrated, following their nutritional requirements. Consequently, the vegetation conditions at the Cradle of Humankind during their migration elsewhere would not be represented in the results of this study. However, the southern African regional palaeoenvironmental signal would prevail.

Seasonality: To know the extent of fossil springbok movements and dietary fluctuations, for all the *Antidorcas* species, according to season is extremely challenging from the current knowledge of the fossil record (as Figure 3.10 for extant springbok). Yet seasonal movements or dietary fluctuations could influence interpretations in this study. For example, if the springbok were to migrate during the 'grazing season', there could be an under-representation of grazing signals in the microwear and isotopic dietary results obtained. It would be difficult to assess whether the under-representation of browsing is the result of a lack of browse at the site or seasonal preference.

In many modern zooarchaeological assemblages, seasonality can be inferred through age at death (e.g. Lubinski 2001). Age at death can be learned from dental eruption patterns and dental enamel wear rates. However, paleontological samples have a high quantity of individual teeth, eliminating eruption patterns from available methods. Wear rates are recorded in this study but require caution as the scale of wear can be species-specific and can vary according to the food consumed. Hard-object feeders are more likely to have greater wear rates than those ruminating on softer foodstuffs.

If there is an over-abundance of similar ages represented within the species assemblage, this can be used to infer seasonality. For example, Dewar et al. (2006) use this method to infer catastrophic mortality profiles for springbok in Namaqualand, as wild springbok in Namaqualand are born within a few weeks in July and there was an over-representation of 6-month-old mandibles within the assemblage, a (December) summer season of death was implied. The microwear signal on the teeth of the individuals in this assemblage could be reliably indicative of the summer diet of the springbok in the area. Alternatively, seasonality has been inferred from dentition in archaeological assemblages by reading the dentin-cementum bands which form seasonally and can be used like tree rings to understand season of death (Speiss 1976; Lieberman 1994). Further investigation into the

feasibility of the method could be considered as an avenue for future research should seasonality be deemed to be a significant factor.

Whilst the visibility of seasonality in the fossil record is poor, by utilising multiple methods, seasonality can be inferred. For instance, seasonality may become apparent from serial sampled stable isotope signals, if sample sizes are sufficiently large to allow accurate interpretations. Additionally, seasonality may be inferred from a discrepancy between dietary indications from a single individual, via stable isotope analysis (young springbok), mesowear (averaged lifetime signal) and microwear analysis (end of life). Additional data, such as the presence of resident browsers (e.g. *Makapania broomi* and *Tragelaphus strepsiceros*) and grazers (e.g. *Damaliscus pygargus*) in each deposit will be factored into this.

Knowledge of seasonal changes adds to palaeoenvironmental interpretations and allows understanding of environmental stressors impacting upon the faunal community. An intensification of the seasons for instance would likely create temporary habitat instability and perhaps lead to rapid adaptation and/ or demise of the more specialist fauna (who, in contrast to generalists, would be more vulnerable to habitat and niche variability).

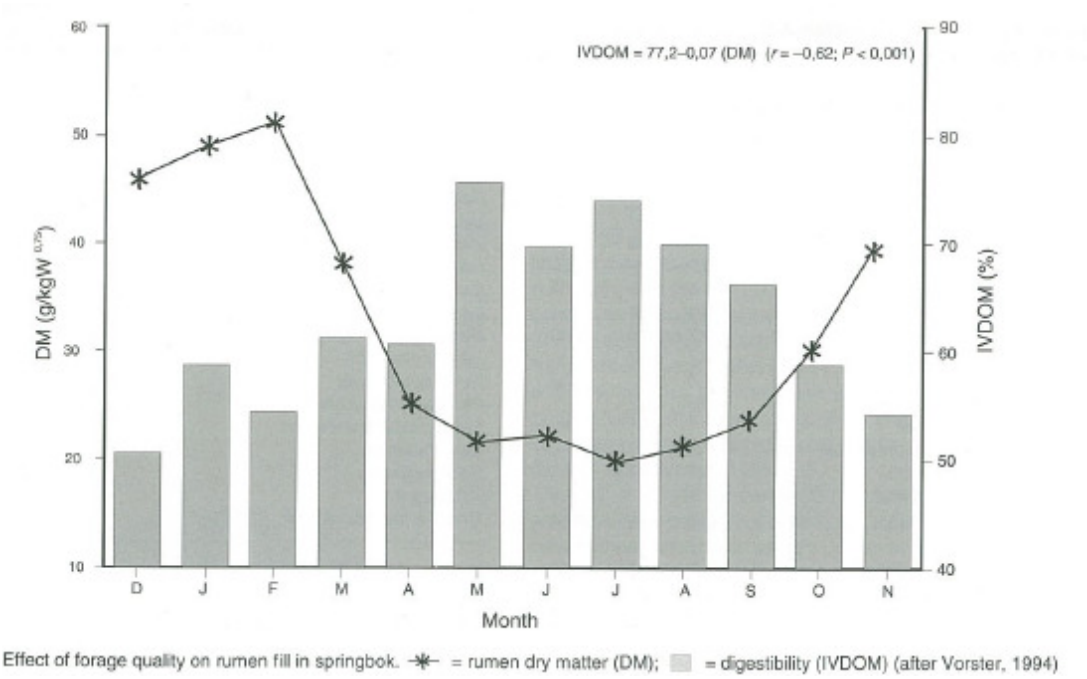


Figure 3.10: From Skinner and Louw 1996, page 22. The impact of seasons on the nutritional requirements of springbok (the rutting season here is in April (Skinner and Louw 1996, page 21)). Vorster's 1994 experiment in the Vrolojkheld Nature Reserve on springbok rumen analysis showed that the springbok preferentially selected young green shrubs and leaves. This preference for the new shoots is inferred for the extinct species, Antidorcas bondi, as the smallest member of a grazing succession (Brink and Lee-Thorp 1992, see below). This information is useful for understanding the ontogeny of the springbok and the potential influencing factors for dietary signals, particularly isotopic values.

3.3 CONTEXT WITHIN THE FAUNAL COMMUNITY and potential biotic causes of dietary change

Associated species

To accurately infer palaeoenvironmental change from palaeovegetation indicators obtainable via *Antidorcas* dentition, considerations regarding the biotic influence on *Antidorcas* diet must be considered. The associated species within the faunal community and their impact on the success of the springbok may not be immediately obvious but undoubtedly existed. For fossil springbok, species within the same assemblage could be inferred as associated (however, due to the complexity of the cave stratigraphy at the Cave of Humankind, this signal is likely further complicated by factors such as time-averaging).

An association exists today between the modern springbok, blue wildebeest, red hartebeest and zebra in parts of Namibia and Botswana (Estes 1991). Observations have been made in the Kalahari, of the blue wildebeest (*Connochaetes taurinus*) preceding the feeding of the springbok; feeding on the higher-level grasses before the lower-level grazing of the springbok (Knight 1995; Stapelberg et al. 2008). However, although these two species are often found together, studies suggest they prefer not to be in close proximity (Stapelberg et al. 2008). This is similar to observations on the Thomson's gazelle (*Gazella thomsonii*) in the Serengeti, with a similar niche partitioning shown with the white-bearded wildebeest (*Connochaetes taurinus maernsi)*, the Thomson's gazelle *(Gazella thomsoni)* and the plains zebra (*equus quagga)* but with increased competition displayed by the wildebeest on the gazelle (Sinclair & Norton-Griffiths 1982).

Furthermore, the Cape buffalo (*Syncerus caffer*) for example, is a known carrier and propagator species of diseases (Michel and Bengis 2012). Hypothetically, if *Antidorcas* were to inhabit areas in close proximity to these buffalo, they would be at increased risk of rinderpest and other zoonotic diseases.

Competitors

Where there is more than one *Antidorcas* species in the same member, they would be expected to have contrasting diets and either occupy contrasting dietary niches or adopt flexibility in their feeding practices. as witnessed in other multi-species taxa, such as Darwin's finches on Daphne Major, Galapagos (Weiner 1994) and as assumed for *Paranthropus* and *Homo* (e.g Robinson 1965). There are many other bovids present throughout the temporal period which would compete with *Antidorcas* species, depending on their respective preferred diets. Key competitors can be more comprehensively appreciated after establishing dietary signals from all *Antidorcas* species.

Figure 3.11 Male impala observed in Pilanesberg National Park, Gauteng Province, South Africa.

MIXED FEEDER: Based on modern comparisons, it could reasonably be assumed that the impala (*Aepyceros melampus*) occupies the most similar niche, and ranges across old and new springbok territories (see

Figure 3.7), and thus may be considered a key competitor to Antidorcas (see Table A5.1, Appendix A5).

The impala appears around 3 Ma at Makapansgat (Reed 1996), then disappears from the South African fossil record, and reappears around 1.8 Ma at Gladysvale (Cradle of Humankind, Gauteng Province, South Africa) (Cooke 1963; Lacruz et al. 2003). If accepting ecological uniformitarianism, one might expect the impala to be more abundant than the springbok during interglacials. The impala and springbok have relatively similar niches (see Appendices A5). However, the springbok is less dependent on water and more arid-adapted than the impala. When considering the requirements of the species, there is the potential that it is not the impala itself impacting upon the community but the changing environmental conditions. The very conditions that draw the impala in could be what pushes other species (especially springbok) out. Therefore, it is not actually inter-specific competition for resources but a response to environmental change. If impala obviously appear when springbok disappear, this would make conclusions simpler to draw.

Potentially dependent fossil species: GRAZING SUCCESSION

Brink and Lee-Thorp (1992)'s suggested grazing system highlights an ecosystem symbiosis, with grazing bovids of varying sizes, cropping grasses according to their size and nutritional demands and become relatively dependent on the other species within this succession. Each animal within this succession would consume a different part of the plant, with the smallest successor, *A. bondi*, eating the shortest shoots and roots, closest to the ground (Brink and Lee-Thorp 1992). If so, it is likely that there would be a substantial amount of grit in the diet, adding to increased wear on the tooth surface, which should show up in the microwear analysis (see chapter 9 'Microwear'). *A. bondi* was proposed as the smallest member of a grazing succession suggested as a result of isotopic analysis combined with morphological and mesowear-type analysis (Brink & Lee-Thorp 1992), supported at other sites, such as Florisbad (Codron et al. 2008).

Within this suggested grazing succession *A. bondi's* diet consisted of high soil moisture, with newly-sprouted grass, thanks to the regular mowing of the 'sward' by larger herbivores and regular moisture would encourage regrowth and thus, sufficient nutrients for *Antidorcas bondi*. (Brink & Lee-Thorp 1992). The nutritional plane is less subject to the seasonal changes under these conditions (Skinner & Louw 1996). A change in moisture level or any palaeoenvironmental/paleovegetational change that impacts any of the other 'facilitator' species in the succession as well as directly *A. bondi*, could impact on *A. bondi*'s success.

Such a scenario is similar to the grazing succession for modern African ungulates proposed by Bell (1971). Further to this, the blue wildebeest (*Connochaetes taurinus*) has been observed to avoid competition with the modern springbok (*Antidorcas marsupialis*) by niche separation (Stapelberg et al. 2008). Knight (1995) suggested the blue wildebeest grazed at a higher level than the springbok, forming a type of grazing succession with the wildebeest preceding the feeding of the springbok. *Connochaetes* sp. has been found in deposits from Sterkfontein Member 4 and Member 5 (East and West) alongside *Antidorcas* sp. as well as in the unstratified D16, D8 and H2 deposits. As is the case for Swartkrans

Member 1 (HR and LB), 2 and 3 (Brain 2004; Reynolds et al. 2003, 2007; de Ruiter 2003; Reynolds & Kibii 2011; McKee et al. 1995). Whilst the same niche partitioning and dietary behaviour may have differed for both *Antidorcas* and *Connochaetes* in the past and differed with the ancestral and varying species, the potential of dependence on other species is worth considering when attempting to understand the evolutionary event potential and influence of environmental and climatic changes in catalysing evolutionary change in the *Antidorcas* lineage (*senso lato*).

Other species within the ecosystem have the potential to buffer the environmental stressors on *Antidorcas*, or conversely, to heighten the competition for desired resources, increasing the impact of palaeoenvironmental changes. It is worth considering the possibility therefore, that these antelope died out as a result of another species due to their dependence on other species within this succession. The beginning of the Holocene saw a decline and extinction of many of these species (Brink and Lee-Thorp 1992). With the ultimate extinction of *A. bondi* occurring at roughly 7000 years ago at the end of the last glacial when environments became wetter (Skinner and Louw 1996), alongside other faunal extinctions.

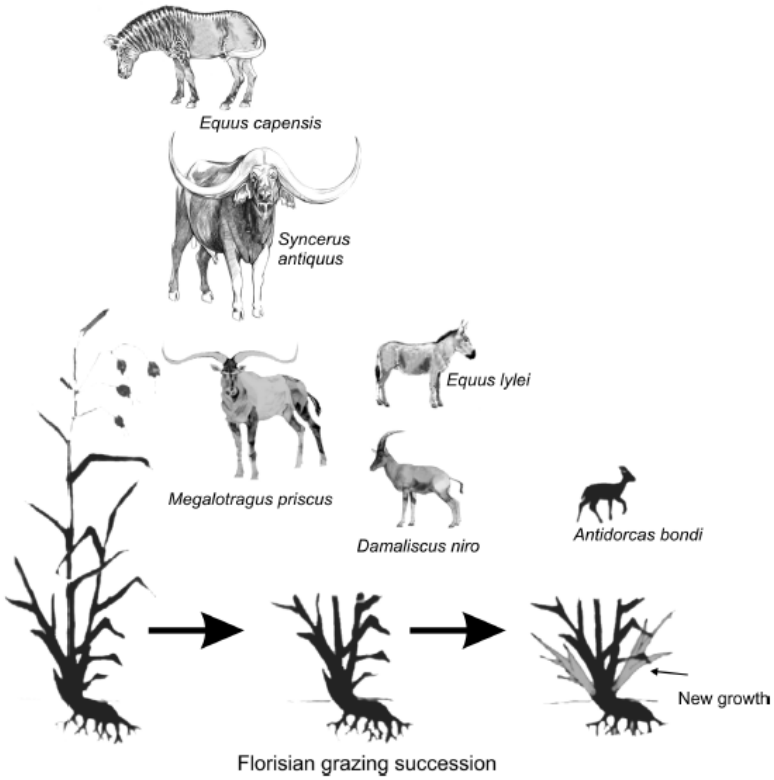


Figure 3.12: Hypothesised Florisian grazing succession including A. bondi as the smallest antelopes forming this succession, Larger-bodied grazers feeding on the longer grass, keeps the grass in a constant state of regrowth, enabling smaller-bodied species to occupy a grazing niche whilst still meetings its nutrient requirements (from Brink 2016, Figure 18.4, p. 298).

Predators

Knowledge of probable predators of fossil *Antidorcas* allows for comprehension of the likely nature of deposition (Cillié 2004).

Table 3.2: Likely predators of springbok, predators present in the same CoH assemblages as Antidorcas. Leopard (Panthera pardus), caracal (Caracal caracal), cheetah (Acinonyx jubatus), lion (Panthera leo), brown hyaena (Hyaena brunnea), African wild dog (Lycaon pictus) and spotted hyaena (Crocuta crocuta). Others, placed in brackets, such as Chasmaporthetes nitidula (and extinct hunting hyaena) are likely to have been predators to Antidorcas based on modern Antidorcas predator (and size) associations. The predators listed with 'modern' refer to know Antidorcas predators. References: Brain 2004, Reynolds et al. 2003, 2007, Reynolds & Kibii 2011, Mckee et al. 1995, deRuiter 2001, 2003.

Member	Predators present
Sterkfontein Member 4	*Panthera pardus, Panthera leo, (Chasmaporthetes nitidula, Chasmaporthetes Silberberg, Homotherium crenatidens)*
Sterkfontein Member 5 West	*Crocuta crocuta, (Homotherium crenatidens, Megantereon cultridens, Chasmaporthetes silberbergi, Chasmaporthetes nitidula)*
Swartkrans Member 1 HR	*Panthera pardus, Caracal caracal, Panthera leo, (Chasmaporthetes nitidula)*
Swartkrans Member 1 LB	*Panthera pardus, Caracal caracal, Acinonyx jubatus Panthera leo, (Chasmaporthetes nitidula)*
Swartkrans Member 2	*Acinonyx jubatus, (Chasmaporthetes nitidula)*
Swartkrans Member 3	*Panthera pardus, Acinonyx jubatus, Crocuta crocuta, (Chasmaporthetes nitidula)*
Modern	*Panthera pardus, Acinonyx jubatus, Crocuta crocuta, Caracal caracal, Panthera leo, Hyaena brunnea, Lycaon pictus*

SECTION 2: SUPPLEMENTARY SPECIES ECOLOGY

GRAZER: Blesbok (*Damaliscus pygargus*)

Figure 3.13: The blesbok (Damaliscus pygargus) pictured with springbok (Antidorcas marsupialis) at the Rhino and Lion Nature Reserve within the Cradle of Humankind World Heritage Site, Gauteng Province, South Africa.

Extant ecology: *Damaliscus pygargus pygargus*, the Bontebok and the Blesbok, *Damaliscus pygargus dorcas* are considered conspecific. *Damaliscus pygargus* is a characteristic species of open grasslands of the southern African Highveld and are considered obligate grazers, with a preference for short grass. They are also obligate drinkers (Lloyd and David 2008).

Fossil *Damaliscus pygargus (dorcas)*: The two modern species of *Damaliscus*, the Blesbok (*Damaliscus pygargus dorcas*) and Tsessebe (*Damaliscus lunatus*) are thought to have diverged very recently with a common ancestor, *Damaliscus agelaius* being found

in fossil form from sites less than 1 Ma in South and East Africa. Kingdon (1997) suggests that this is due to the emergence of a new competitor taking over as the dominant grazer in dry savannah grasslands.

D. dorcas was found at the cradle of Humankind sites but its geographical range no longer extends this far and is confined to small areas in the southern half of South Africa (Estes 1991). The Tsessebe (*Damaliscus lunatus*) inhabits floodplain areas, where small, isolated populations appear to be vulnerable to environmental changes (Kingdon 1997 p.427; Estes 1991). Some *D. lunatus* teeth are likely to be included in the fossil *Damliscus* sp. (undintified beyond genus level) category from the Cradle of Humankind assemblages. A small selection of modern *D. lunatus* were included in the dataset for comparison to these fossil examples (see Appendix A7).

BROWSER: Greater Kudu (*Tragelaphus strepsiceros*)

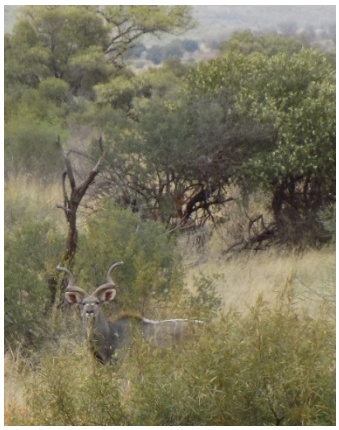


Figure 3.14: Male greater kudu observed in Pilanesberg National Park, Gauteng Province, South Africa, surrounded by tall trees and browse vegetation.

Extant ecology: Preferred habitats include mixed scrub woodland, acacia, and mopane bush on lowlands/highlands. Greater kudus are considered obligate browsers, independent of water unless the vegetation is very dry (Owen-Smith 2013).

Fossil *Tragelaphus strepsiceros*: The Greater kudu is found extensively across South Africa and throughout the deposits of Sterkfontein and Swartkrans but in relatively low numbers. Typically, the greater kudu feeds preferentially on browse (Estes 1991; Castelló 2016).

CHAPTER 4

MATERIALS AND METHODS

SECTION 1: MATERIALS

A selection of *Antidorcas*, and supplementary taxa of *Damaliscus pygargus* and *Tragelaphus strepsiceros* dentition was used from the Cradle of Humankind site assemblages (

Table 4.1), as well as a selection of comparative modern dentition from each of these taxa.

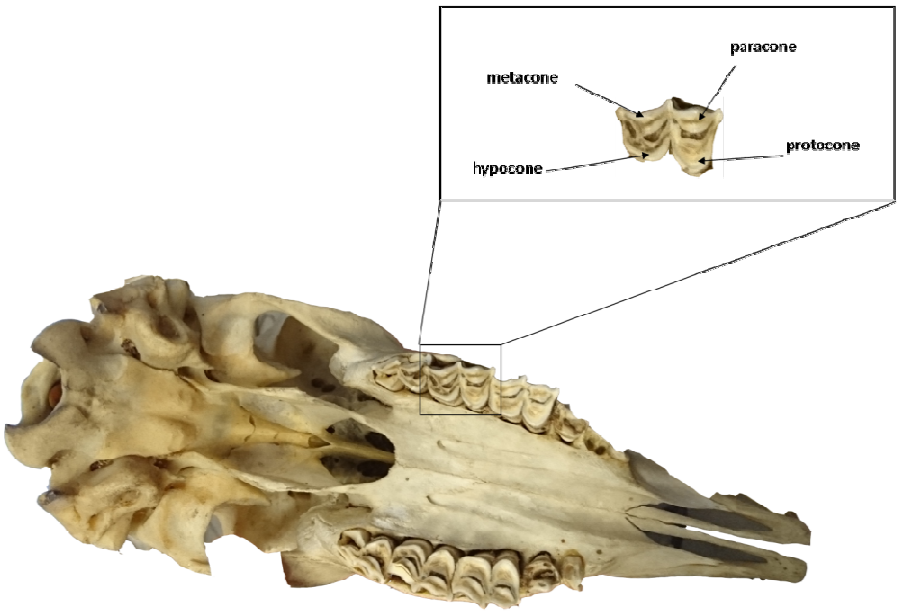


Figure 4.1: University of the Witwatersrand, BPI comparative collection: Antidorcas marsupialis cranium with facet identification for maxillary (upper) molars.

Selection Criteria: The selection criteria used for each method, including minimum number of individuals, tooth type, species, tooth characteristic and quality, are discussed individually for each method used in the Methods section (section 2) below.

Main site assemblages:

Sterkfontein (Member 4, Member 5 East, 5 West and StW53 Infill), Swartkrans (Member 1 lower breccia, hanging remnant, Member 2 and Member 3), Kromdraai (KA, KB, KE and KW specimens) and Cave of Hearths (COH Beds 1-3, unstratified and Bed 9).

Additional site assemblages used (fewer *Antidorcas* specimens used):

Sterkfontein unstratified, Sterkfontein L63, Gondolin GDA, Gladysvale and Plovers Lake

Further faunal assemblages from additional sites were used for a meta-analysis (chapter 4) of southern African hominin-associated deposits from within this timeframe (2.8-0.8 Ma). These are briefly discussed.

Chronology and Acronyms used

Before using the data collected, the provenance of the material must be considered. Published dates and relative chronologies will be relied upon. All conclusions are subject to revision should these dates be amended. Within this research, the following chronological order (from oldest to youngest) for deposits is used to represent a temporal sequence:

Sterkfontein Member 4 (SK M4); Kromdraai W, B and E (KW, KB, KE); Sterkfontein Member 5 (SK M5) StW53 Infill (SK M5StW), East (SK M5E) and West (SK M5W); Swartkrans Member 1 (SKX M1) Lower Bank (LB) and Hanging Remnant (HR); Kromdraai A (KA); Gondolin (GA); Swartkrans Member 2 (SKX M2); Cooper's Cave (CC); Swarktrans Member 3 (SKX M3); Plovers Lake (PL); Cave of Hearths (COH), Gladysvale (GV) and Modern.

Specimens used

Full specimen lists are provided in Appendices (Appendix A10).

Table 4.1: Fossil and modern specimens used for this research, separated by site, context (Member), and taxa. N= number of specimens used. Each specimen may be represented by more than one tooth (detailed in Appendix A10).

SITE	MEMBER	GENUS	SPECIES	N
Sterkfontein	4	*Antidorcas*	(total)	13
		Antidorcas	*recki*	12
		Antidorcas	*bondi*	1
		Damaliscus	*pygargus*	8
		Tragelaphus	*strepsiceros*	6
	5	*Antidorcas*	(total)	59
	5 West	*Antidorcas*	*recki*	14
		Antidorcas	*bondi*	24
		Antidorcas	*marsupialis*	2
		Antidorcas	sp.	1
		Damaliscus	*pygargus*	10
		Damaliscus	sp.	2
	5 East	*Antidorcas*	*recki*	6
		Antidorcas	*bondi*	8
		Antidorcas	*marsupialis*	2
		Antidorcas	sp.	2
		Damaliscus	*pygargus*	9
		Damaliscus	sp.	13
		Tragelaphus	*strepsiceros*	3
	StW53 Infill	*Damaliscus*	*pygargus*	3
		Tragelaphus	*strepsiceros*	2
	L/63/ PM6 Infill	*Antidorcas*	*marsupialis*	12
		Damaliscus	*pygargus*	6
Swartkrans	1	(total)		29
		Antidorcas	(total)	25
		Antidorcas	sp.	4
		Antidorcas	*recki*	4
		Antidorcas	*bondi*	3
		Antidorcas	*marsupialis*	14
		Damaliscus	*pygargus*	4
	1, Hanging Remnant	(total)		5
		Antidorcas	sp.	1
		Antidorcas	*bondi*	2
		Tragelaphus	*strepsiceros*	2
	1, Lower Bank	(total)		13
		Antidorcas	sp.	2
		Antidorcas	*recki*	3
		Antidorcas	*bondi*	1
		Antidorcas	*marsupialis*	6
		Damaliscus	*pygargus*	1
	2	(total)		99
		Antidorcas	(total)	82
		Antidorcas	sp.	28
		Antidorcas	*recki*	7
		Antidorcas	*bondi*	36
		Antidorcas	*marsupialis*	11
		Damaliscus	*pygargus*	8
		Tragelaphus	*strepsiceros*	9
	3	(total)		118
		Antidorcas	(total)	116
		Antidorcas	sp.	15
		Antidorcas	*cf. recki*	24
		Antidorcas	*bondi*	4
		Antidorcas	*marsupialis*	73
		Damaliscus	*pygargus*	2
Kromdraai	(total)			69
Kromdraai		*Antidorcas*	(total)	57
	KA	*Antidorcas*	sp.	37
		Damaliscus	sp.	12

	KB	*Antidorcas*	sp.	1
		Damaliscus	sp.	3
	KE	*Antidorcas*	sp.	3
	KW	*Antidorcas*	sp.	16
Cave of Hearths	(total)			70
Cave of Hearths	*see text below	*Antidorcas*	sp.	8
		Antidorcas	*bondi*	45
		Antidorcas	*marsupialis*	13
		Tragelpahus	*strepsiceros*	2
		Aepyceros	*melampus*	2
Gondolin		*Antidorcas*	sp.	2
		Damaliscus	sp.	1
Plovers Lake		*Antidorcas*	sp.	32
Gladysvale	(total)			12
Gladysvale		*Antidorcas*	sp.	2
		cf. Antidorcas		1
		Damaliscus		7
		Tragelaphus		2
Modern		*Antidorcas*	*marsupialis*	43
		Damaliscus	*pygargus*	31
		Damaliscus	other	10
		Tragelaphus	*strepsiceros*	10

Further information on specimens used

Sterkfontein and Swartkrans faunal collections used for this research were previously curated at the Ditsong Museum of Natural History (2016 data collection only) but are currently, at the ESI, University of the Witwatersrand (2017 data collection).

Kromdraai faunal collections used for this research are curated at the Ditsong Museum of Natural History (pre-2014) and the ESI, University of the Witwatersrand (2014 onwards, labelled with the prefix 'KW'). KW and the few KB and KE specimens are positioned on the timeline between Sterkfontein Member 4 and Sterkfontein Member 5. KA and KB are no longer justified prefixes as these represent a mix of stratigraphic units that are not temporally homogeneous. [KB and KE specimens used here were checked against current records held (ESI, University of the Witwatersrand, Zipfel pers comm.) to place them in the appropriate chronology. Of those recorded, the *Antidorcas* specimens, KE 7196 was found at the base of the flowstone (Bas Coulée Stalagmitique) and KE 7257, KE 6939 were found on the West Portos Wall/ Brain Trench (Edge and North respectively)]. Pending refinement of member temporal ranges and clarification on provenance of individual KW specimens, Kromdraai deposits' specimens here are placed between those of Sterkfontein Member 4 and Sterkfontein Member 5 / Swartkrans Member 1 in the chronological succession used in this research to represent change through time. KA (1.5-1 Ma) is positioned between Swartkrans Member 1 and Swartkrans Member 2 in the chronological sequence applied here.

The Cave of Hearths, Plovers Lake, Gladysvale and Gondolin faunal assemblages are curated at the ESI, University of the Witwatersrand. A very small sample size is represented from Gondolin.

Although outside the main geographic focus of this research (Cradle of Humankind, CoH), hominins and *Antidorcas* were present at the Cave of Hearths (COH), which represents the youngest deposit used as a focus site for this research. Including this site enables

consideration of a wider geographic area, incorporating more vegetation and habitat types. Faunal assemblages considered here are primarily from Beds 1-3, believed to be ESA (early stone age) deposits. *Antidorcas* remains have been recovered from surface finds, unknown stratification, Bed 3 and Beds 8/9 and are subject to the multi-method analysis of this research dataset* (see

Table 4.1).

At c. 0.08 Ma, the internal deposit of Plovers Lake is beyond the youngest limit considered for this research and are used here primarily as a relatively 'modern' comparisons for fossil *Antidorcas* palaeoecology.

A selection of modern specimens were measured to establish the intra-specific variation levels for an *Antidorcas* species (and for supplementary species of *Damaliscus* and *Tragelaphus*). All information held by the housing institution was recorded to allow for detailed interpretation of findings. Information such as where the animal lived -country, geographic area, wild/zoo specimen; date killed/died and sex of the individual. Priority was given to wild-caught individuals. Zoo specimens were avoided as far as possible as they are not reflective of a natural diet.

SECTION 2: METHODS

A faunal meta-analysis and *Antidorcas* identification methods are introduced first to establish the baseline from which the majority of this research depends. The main methods used in this research to assess palaeoenvironmental reconstructions and changes are then introduced, how the methods have been used to date (as available from the literature) is summarised and evaluated and the sampling strategy and the particular method implemented here is provided.

4.1 Faunal Community Meta-analysis

Published faunal assemblage records (cited in chapter 5) are used to establish the fossil faunal community for each site and stratigraphic unit member to assess the environmental signal suggested by the entire faunal community. For example, an assemblage dominated by grassland taxa could be indicative of grassland-dominated habitats (Vrba 1980), consequently we may expect *Antidorcas'* dietary behaviour to reflect increased grassland. This not only gives an expected signal as a starting point but allows the assessment of *Antidorcas* as a bioproxy (i.e. by comparing the final *Antidorcas* results with those gained from the entire faunal community). The more detailed vegetation picture and temporal changes of such are then gained from *Antidorcas* data from this research.

Lists of recorded taxa for faunal assemblages from contemporary South African sites were compiled. All sites falling between 3.0-0.5 Ma were considered. Those with adequately recorded and freely-available published faunal data were used for this analysis. Due to the variability in published faunal records, presence/absence data at genus level was used for the main focus of this meta-analysis. For the purposes of this study, presence/absence is

appropriate as only an indication of similarity is required. It is provided as background to the research, rather than a fundamental aspect of the research.

Various linkage methods were trialled to assess the most representative method to implement here as are discussed in more depth in chapter 5.

4.2 Taxonomic Identification Methods

Identifying dental remains to genera in mixed bovid fossil assemblages can be challenging (e.g. Brophy et al. 2014) and attempting to identify to species level even more so. Specimens are often represented by isolated molars, making many of the characteristic species' discrete traits of the masticatory apparatus invisible from the specimens. An overview of the concept of what constitutes a species is discussed in Appendix A5. This section provides a breakdown of how taxonomy was determined for the dentition used in this research. Although taxonomic identification of fossil *Antidorcas* is most easily differentiated with horncores, horncore and dental specimens were rarely relatable to one another due to the nature of the fossil deposits and horncore remains were relatively sparse. Focus is given to the dental remains due to their dietary indication potential. The question of horncores is addressed separately in Appendix A4 and not does not form a central part of this research.

The identification of *Antidorcas* dental specimens underpins the analysis in this research. In the absence of a more in-depth taxonomic-focused research for the *Antidorcas* fossil record, the basic taxonomic identification requirements are covered here (see results chapter 6, section 2) in order to accurately utilise the *Antidorcas* material.

RATIONALE: Where dietary responses may be inferred to be indicative of palaeoenvironmental change, knowledge of species is crucial. In order to see any dietary changes that may reflect differential palaeovegetation availability, one must first acknowledge which species is represented by the specimen, to know which specimens to accurately group together to determine species' diet, and then, how this diet changes through time. Species need to be identified as far as possible to ensure this vegetation signal is a true reflection of palaeovegetation availability change and not skewed, for instance due to an over-abundance of *A. bondi* within the *'Antidorcas'* sample, in favour of increased grassland. Closely related bovid taxa often have differing ecological requirements, as is true of the fossil springbok species. Therefore, inaccurate identifications could have ramifications when reconstructing Palaeoenvironments (Brophy et al. 2014).

Antidorcas australis?

In addition to the established species categories of *A. recki*, *A. bondi* and *A. marsupialis*, a potential fourth species, of unknown palaeoecology, *Antidorcas australis* has been contentiously suggested (Hendey and Hendey 1968). It remains unclear as to the geographic and temporal range of this fourth 'species', being perhaps only a Cape endemic, although suggested to be present in Swartkrans (e.g. Vrba 1973). The taxonomic level of *A. australis* is also open for debate, representing perhaps only a sub-species or even regional population. As Gentry (2010) points out, the likelihood of three, let alone, four species of one genus present at any one time, in a geographically restricted area seems unlikely.

Method of differential identification of *Antidorcas* dentition

Images of antelopes with similar dental morphology, likely to be found within the same assemblage are provided below (Figure 4.4). *Antidorcas* can be differentially identified from other similar bovids by the following features (as outlined by Gentry 1966, 2010; Vrba 1970; Groves 2000):

- *Antidorcas* has 5 pairs of grinding teeth, as opposed to 6 pairs characteristic of *Gazella* (Cain et al. 2004).
- Styles (Figure 4.2) of maxillary molars appear more pronounced than in *Gazella*.
- Lower molars have straight lingual walls. The mandibular molar buccal midwall stylids are a derived characteristic of *Antidorcas* dentition.
- Premolar row is reduced and P_2 is often absent.
- Small P_3 and functional P_4, whilst P_1 is phylogenetically lost (Skinner & Louw 1996) in the adult dentition.

Antidorcas adult dental formula is the same for all extinct and extant species: $I\frac{0}{3}C\frac{1}{1}P\frac{3}{3}M\frac{3}{3}$

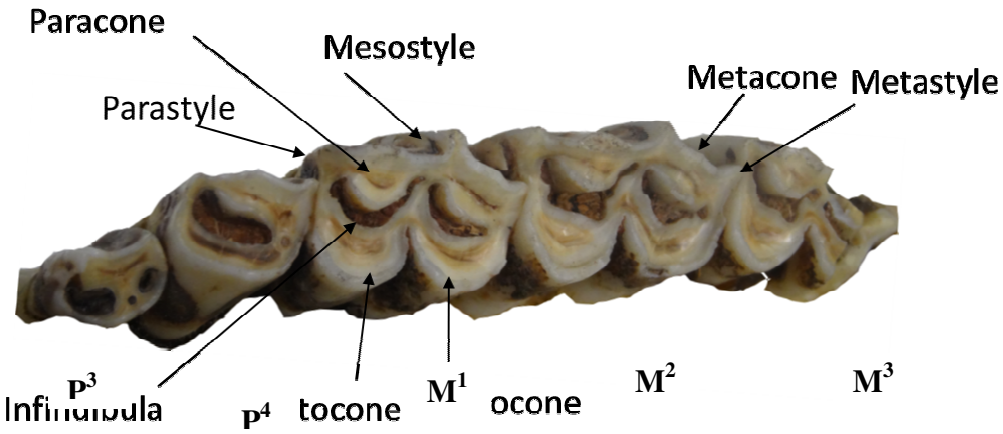


Figure 4.2: Dental nomenclature used for upper (maxillary) molars. P= premolar, M= Molar.

Taxonomic Identification of *Antidorcas* Specimens

The question of taxonomic identity of many of the *Antidorcas* specimens will be addressed and clarified, where possible, within this research. *Antidorcas* species characteristics are summarised in Table 4.2. Dental specimens assigned in published sources to '*Antidorcas* sp' (Brain 1981; Reynolds 2005) or '*Antidorcas australis'* are reconsidered here for taxonomic assignment. The label of '*Antidorcas* sp.' was also given if conflicts arose between published sources (e.g. Vrba 1973; de Ruiter 2001, 2003) identifications or between personal identifications and published sources. Reassignments are based on visual observation and comparison with modern specimens and comparative collections (at the ESI, University of the Witwatersrand).

Antidorcas australis dentition was originally differentiated primarily on being slightly more gracile with narrower molars (Vrba 1973). That there is likely to be overlap of smaller male *A. australis* and larger female *A. marsupialis* individuals; and with larger *A. recki* and smaller *A. marsupialis* due to being potentially a chronospecies (transitional form between *A. recki* and *A. marsupialis*) further complicates accurate species identification. Visual assessments were made without prior knowledge of previous published taxonomic assignments. For initial, visual taxonomic classifications, no differentiation was made

between *A. marsupialis* and *A. australis*. Instead, these specimens were grouped as '*A. marsupialis / australis'* to establish taxonomy without *a priori* assumptions, as it is acknowledged that visually *A. australis* dentition are almost indistinguishable from fossil *A. marsupialis* (Hendey & Hendey 1968).

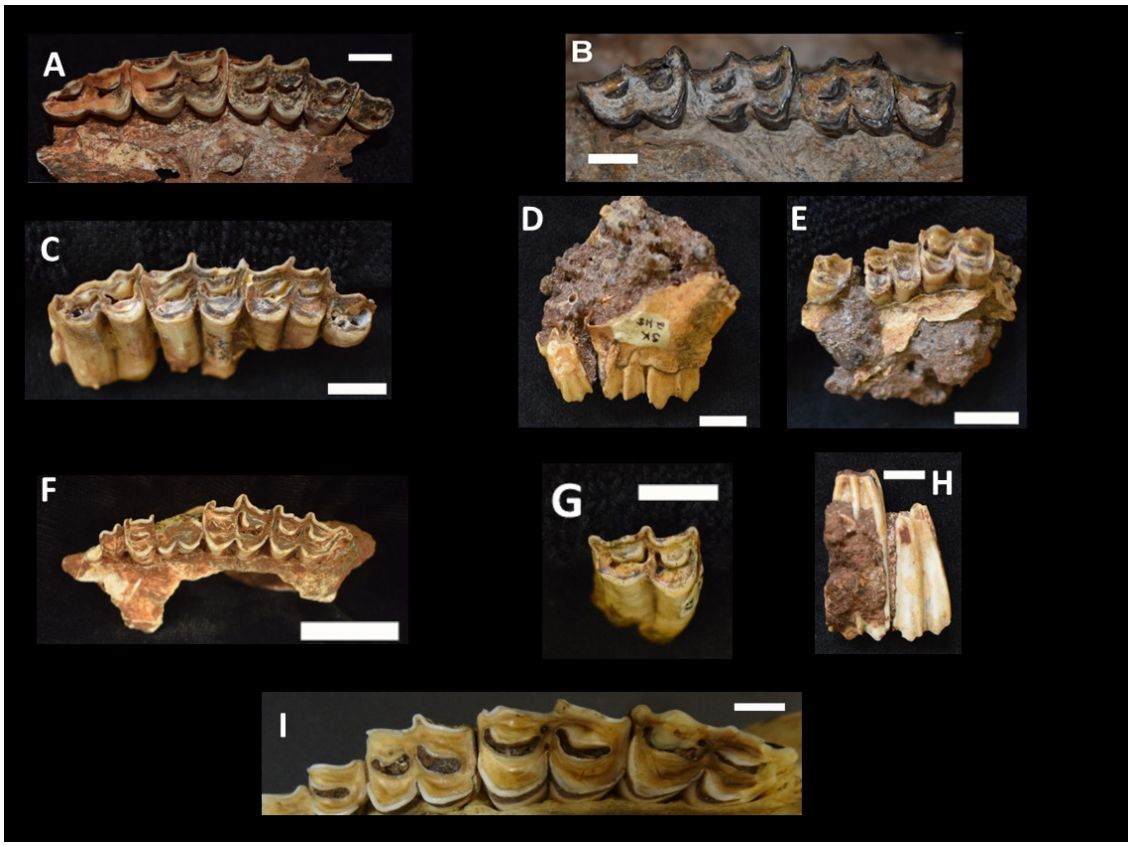


Figure 4.3:Examples of Antidorcas maxillary (upper) dentition. A-B: Antidorcas recki (A=KA2610; B=KNM-ER 6-18 [KNM-ER 6-18 photographed by Lucile Crété]), C-E: Antidorcas australis as identified by Vrba (1973): (C=SK 3055; D and E=SK 2115), F-H: Antidorcas bondi (F=SF 592; G=KA 2472; H=SK 2366), I: modern Antidorcas marsupialis. [Key: KA= Kromdraai, KNM-ER=Kenya National Museum-East Rudolph, SK= Swartkrans, SF= Sterkfontein]. Scale bars equal 10mm. Figure from Sewell et al. 2019 (p. 4, Figure 1).

Table 4.2:Features typical of each Antidorcas species found in Southern Africa, used to aid in species identification of fossil dentition. Characteristic features used to establish taxonomic assignment of fossil dental specimens (Vrba 1973; Cooke 1996; Cooke & Wells 1951; Brain 1983; de Ruiter 2003; Gentry 1978, 2011, 2010). Typical M2 dimensions established according to the type specimens, from corresponding reference as stated in the table. 1 Cooke &Wells 1951; dimensions written as length x breadth (in mm). 2 mesiodistal length x bucco-lingual width. Based on mean measurements taken of A. recki from Sterkfontein and Swartkrans by L. Sewell (2016). 3Vrba 1970; mesiodistal length taken from the mesial surface of the parastyle to the distal surface of the metastyle x mean value from modern A. marsupialis specimens (measured by L. Sewell). 4 Based on mean measurements (by L. Sewell and Vrba 1973) of specimens assigned to A. australis; mesiodistal length x buccolingual width. Table from Sewell et al. (2018). Text in bold indicates where dental measurements can support visual taxonomic identifications.

Species	***Antidorcas bondi***	***Antidorcas recki***	***Antidorcas marsupialis***	***Antidorcas cf. australis***
Reference	Cooke & Wells 1951	Schwarz 1932	Zimmermann 1780	Hendey & Hendey 1968
Figure	See Figure 4.3, Images F-H	See Figure 4.3, Images A-B	See Figure 4.3, Image I	See Figure 4.3, Images C-E
Characteristic dental features	• Upper: Strongly developed styles on buccal walls (are often basally (i.e. towards the body of the tooth) pinched, giving a more prominent impression). • Upper: Strong external ribs (thickened enamel lingual surface). • Upper: Complicated folding of enamel walls of central cavities, with a greater tendency towards dumbbell- shaped central cavities (infundibula) and increased curvature. • Molar lingual walls have a strong, undulating aspect. • Outside enamel edges typically 'wavier' than the flattened appearance of those in *A. marsupialis*.	• Unbent central cavities (U-shaped infundibula) • Straight mandibular lingual molar face • Buccal lophs are V-shaped (more so than the more rounded ones of *A. marsupialis*) • Has styles on upper molars, which are more often V-shaped. Concave labial walls behind their mesostyles a flatter, even concave, wall between the mesostyle and metastyle. • Upper: Less strongly pronounced concave posterior part of lateral wall (than in *A. marsupialis/ A.*	• Lower: Lingual walls are straight and almost flat in mandibular molars (less outwardly bowed than in the impala). • Lower: Central cavities straighten in relatively early wear stages • Large M_3 metastyle, with noticeably enlarge third (hypoconulid) lobes • Lacks PM_2 • Reduced PM_3 • Uncomplicated infundibula (unlike *A. bondi*)	• Molars are bucco-lingually narrower in mesiodistal length (Vrba 1973) than *A. marsupialis* (Vrba 1970) • Lower: Central cavities straighten in relatively early wear stages • Large M_3 metastyle. • Lacks PM_2 • Reduced PM_3 • **Narrower than *A. marsupialis* and appear more gracile (Vrba 1970)**

• Extreme hypsodonty (tall teeth) • Hypsodonty index for M2 was higher at all wear stages than in other species of *Antidorcas*. • **Teeth narrow relative to length**. • Similar to impala but transversely narrower. • Lower: a depression runs from occlusal surface to root between lingual molar lobes. Adjacent to these depressions the molar walls appear to "bow out", giving the whole lingual molar edge a wavy look (more similar to impala than the other *Antidorcas* species). • Lower: Sometimes present: lingual "rib" (metastylid) in the or depression between molar lobes. • Lower: Central cavities are centrally constricted, creating a dumbbell appearance. • Large M_3 metastyle. • Typically Retains PM_2 • PM_3 is larger and more complex than in *A. marsupialis.* • Buccal lobes of lower molars are generally more pointed (less 'squaring'-where the anterior part of the lobe approaches the lobe in front), than is the case in the other *Antidorcas* species. The same for the lingual walls of upper molars.	*bondi*). • Upper: Stronger styles than *A. marsupialis*, with a flatter and even concave wall between mesostyle and metastyle. • P_2 is usually retained (sometimes absent). • Lower: Central cavities straighten in relatively early wear stages. • Lower: lingual walls of lower molars are almost as flat as in *A. marsupialis* • Large M_3 metastyle. • Typically Retains PM_2 • PM_3 is larger and more complex than in *A. marsupialis.*	• Typically, slightly larger in overall occlusal dimensions than *A. recki.*

	• Lower: Occasionally goat folds/basal pillars are present (extra folds on the anterior-posterior aspect of the tooth), characteristic of goat molars. • **Thickness of enamel; enamel walls, especially those surrounding central cavities (infundibula) typically appear thicker** with respect to tooth size than is the case in other *Antidorcas* species. • Lower: Fused paraconid and metaconid.			
Mean M^2 dimensions	[1]16mmx9mm	[2]13.3mmx6.3mm	[3]17.4mm(Female)18mm (Male)x 10.9mm	[4]12.5mmx7.95mm

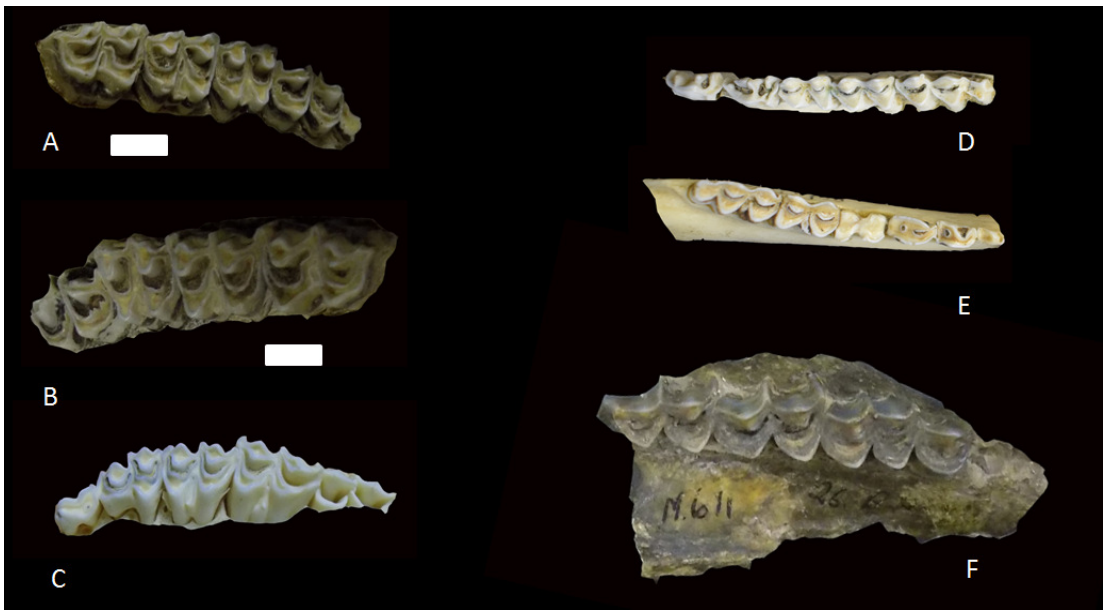


Figure 4.4: Dentition with similar morphology to Antidorcas, likely to found in the assemblages at the Cradle of Humankind to assist with differential identification of Antidorcas dentition. A-C: Redunca arundinium (Reedbuck) maxillary dentition, Distong Museum of Natural History Mammology department; D-E: Tragelaphus scriptus (Bushbuck) mandibular dentition, University of the Witwatersrand BPI comparative collection; F: Gazella vanhoepeni (fossil) M611 right maxilla, University of the Witwatersrand BPI comparative collection.

4.2.2 *Antidorcas recki* morphology

The ancestral springbok was smaller than the descendant springbok, with proportionally shorter legs, possessing horncores that were bent sharply backwards distally, with more mediolateral compression than *A. marsupialis* (Brain 1993; Gentry 2010). The horncores recovered from Olduvai showed great variation, all with thicker bases than Gazella but with some individual specimens' horncores being shorter and tapering rapidly to a point, with no flattened lateral surface or transverse ridges (Gentry 2011).

The morphology of *A. recki* recovered from Kromdraai A is believed to differ slightly from that of the Swartkrans, Gondolin and East African (Olduvai Bed 1) *A. recki* (Herries et al. 2009; Vrba 1973, 1976; Gentry & Gentry 1978; Adams & Conroy 2005). As alluded to previously and stated by Vrba (1976), *Antidorcas* morphology has little clear succession and a broad time span across both East and southern Africa. *Antidorcas recki* was however, the first *Antidorcas* species recognised outside southern Africa (Gentry 2010).

Characteristic dentition features for *A. recki*

Figure 4.5: A. recki Sterkfontein Member 4. Specimen number: STS 1944; Mandible fragment with M_{2-3} in situ. From left to right: lingual, buccal and occlusal views (lower image). Scale bar represents 10mm.

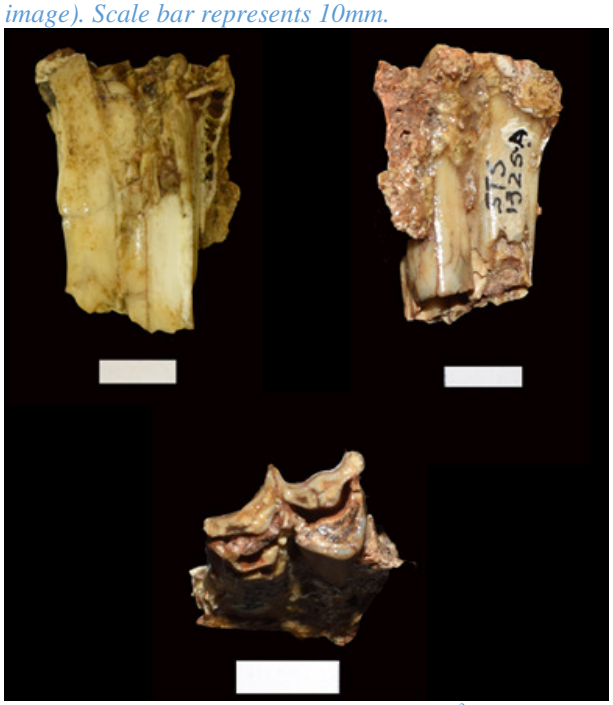


Figure 4.6: A. recki maxillary molar (M^3). Specimen number: STS 1325(a). Sterkfontein Member 4. From left: buccal, lingual and occlusal (lower image) views. Scale bar represents 10mm.

4.2.3 *Antidorcas bondi* morphology

A. bondi was shorter but sturdier than the extant *A. marsupialis* (Plug and Peters 1991). Skeletal features of the ulna, proximal radius, os carpi, phalanges, metapodials and distal humerus can be used to distinguish *A. bondi* from *A. marsupialis* postcranially (Plug and Peters 1991).

Characteristic dentition features for *A. bondi*

A. bondi is the most readily differentiated fossil *Antidorcas* species from dental remains.

Figure 4.7: A. bondi Sterkfontein Member 5 East Specimen number: SF 1799 M^2. From left: buccal, lingual and occlusal (lower image) views. Scale bar represents 10 mm.

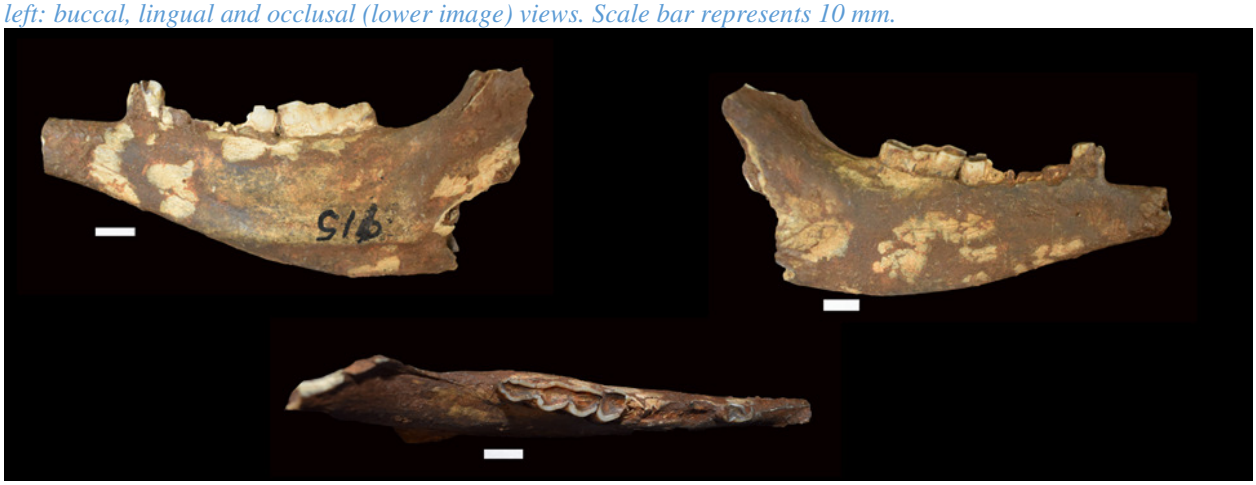


Figure 4.8: A. bondi Sterkfontein Member 5 West. Specimen number: SF 915 mandible fragment with M_3 in situ. From left: lingual, buccal and occlusal (lower image) views. Scale bar represents 10 mm.

4.2.4 *Antidorcas marsupialis* morphology

A. marsupialis evolved from *A. recki* (Vrba 1973; Brain 1981) yet a clear FAD for *A. marsupialis* has not been established, in part due to the taxonomic uncertainty of *Antidorcas australis*. Although dentally and postcranially, *A. recki* was smaller (Vrba 1974) and *A. marsupialis* has been proposed as the largest bodied *Antidorcas* (conforming to Cope' rule), with large M_3 displaying enlarged hypoconulid (third) lobes. From dentition, fossil *A. marsupialis* is difficult to distinguish from the ancestral *A. recki*. This is particularly true for early forms, and perhaps exacerbated by sexual dimorphism in both *A. recki* and *A. marsupialis* resulting in size overlap from large females of *A. recki* and small males of *A. marsupuialis*.

Characteristic dentition features for *Antidorcas marsupialis*

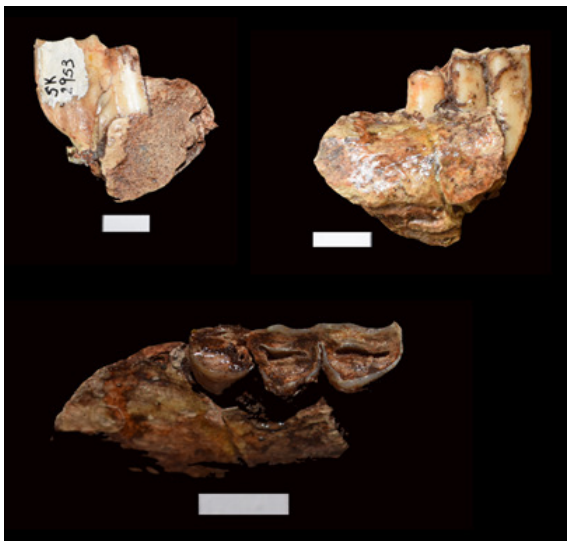


Figure 4.9: A. marsupialis Swartkrans Member 2. Specimen number: SK 2953. M_3 in mandible fragment. From left: lingual, buccal and occlusal (lower image) views. Scale bar represents 10 mm.

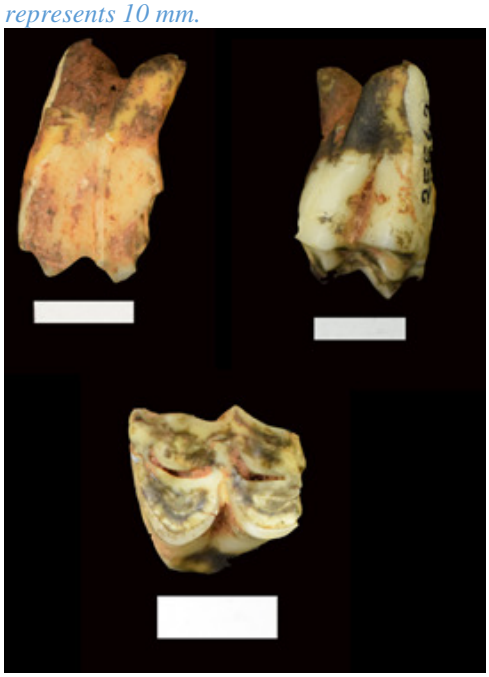


Figure 4.10: A. marsupialis Swartkrans Member 3 Specimen number: SKX 25562 isolated LM^1. From left: buccal, lingual and occlusal (lower image) views. Scale bar represents 10mm.

4.2.5 Supplementary Species

A) THE BROWSING END OF THE DIETARY SPECTRUM

Tragelaphus strepsiceros **Images of molars**

UPPER DENTITION

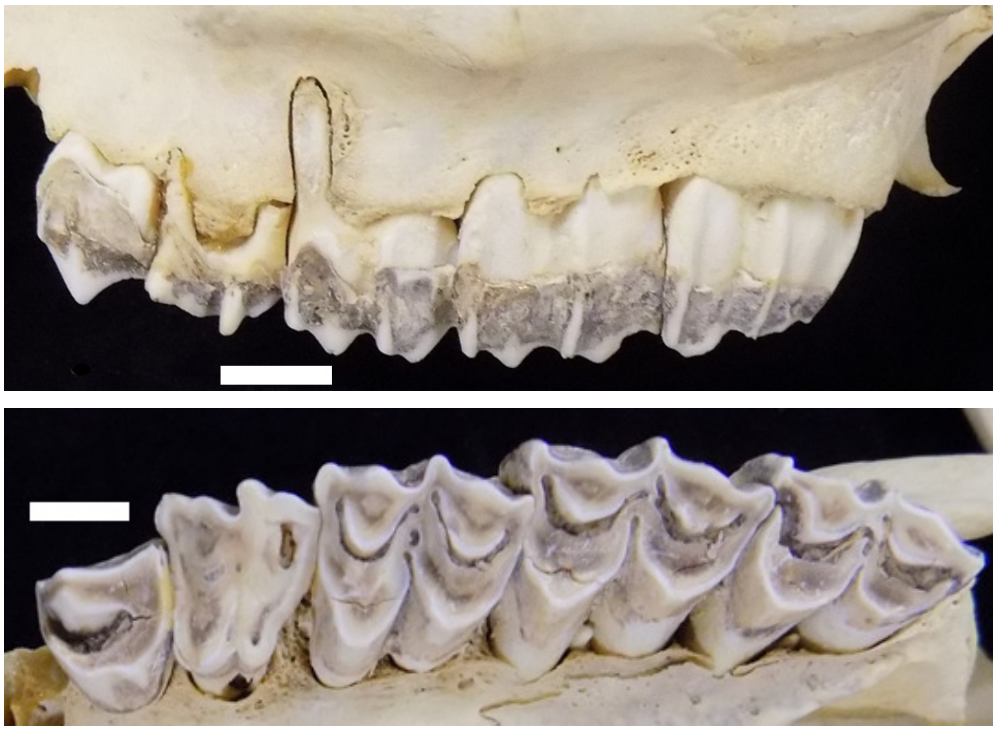


Figure 4.11: South African female Greater kudu (Tragelaphus strepsiceros) maxillary dentition in buccal view (upper image) and occlusal view (lower image). Specimen number: AZ 1261 (curated at the Ditsong Museum of Natural Hisotry, Pretoria). Scale bar equals 2cm.

LOWER DENTITION

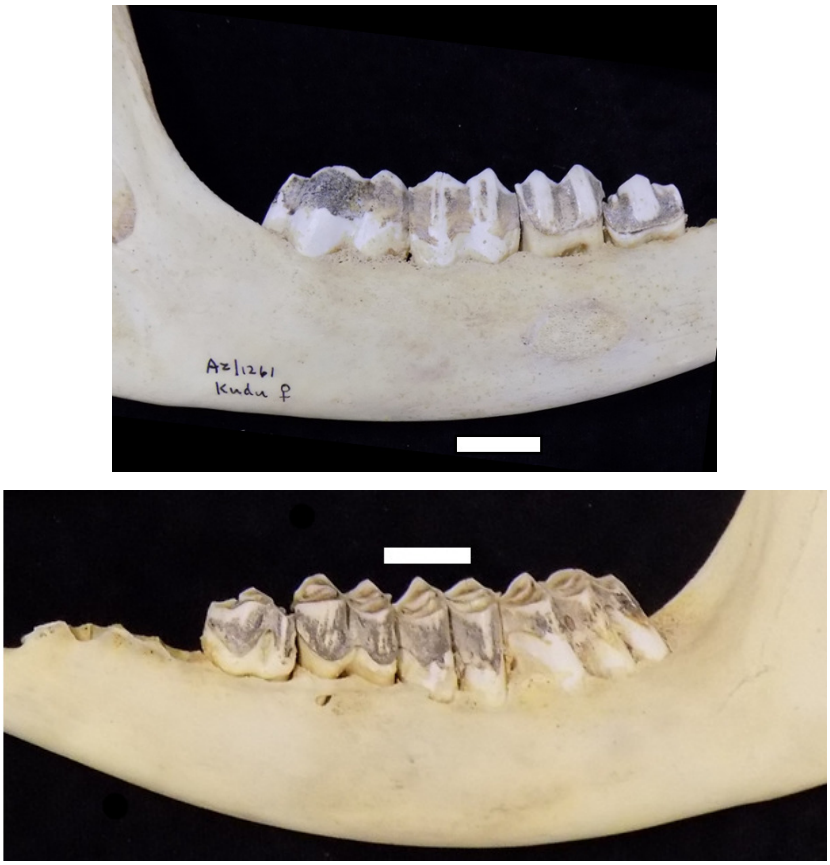


Figure 4.12: South African female Greater kudu (Tragelaphus strepsiceros) mandibular dentition, lingual (upper image) and buccal (lower image) views. Specimen number: AZ 1261 (curated at the Ditsong Museum of Natural History, Pretoria). Scale bar equals 2cm.

B) THE GRAZING END OF THE SPECTRUM

Damaliscus pygargus **Images of molars**

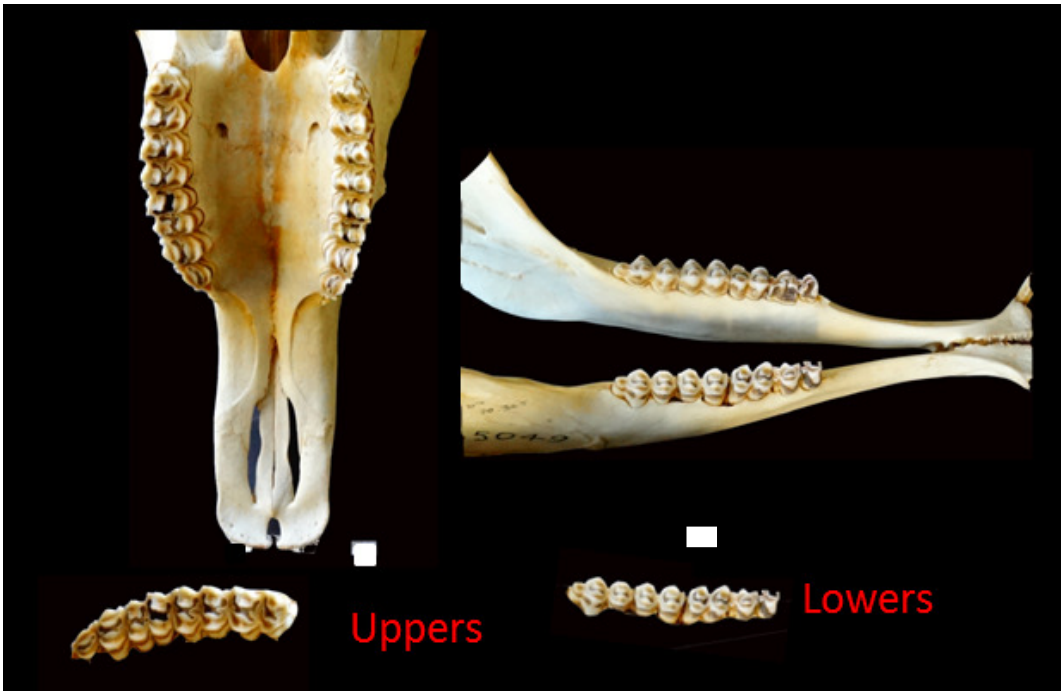


Figure 4.13: NHM.70.345 Damaliscus pygargus dorcas maxilla (left) and mandible (right). Scale bar equals 10mm.

4.2.6 Assessing the TAXONOMY of the Cradle of Humankind *ANTIDORCAS AUSTRALIS*

Whether the '*A. australis*' dental specimens (identified by Vrba 1973 from the Cradle of Humankind fossil sites, and also measured in this study) align with any particular *Antidorcas* taxa is assessed in the '*Antidorcas* results' chapter (chapter 6). Of the Cradle of Humankind (Sterkftonein, Swartkrans and Kromdraai) assemblages, some of the specimens previously assigned to *A. australis* (Vrba 1973), and used within this research, were separated for this targeted investigation. Results are drawn from each of the methods (linear dental measurements, enamel thickness, mesowear, microwear and isotopes) later implemented for the palaeoenvironmental investigation.

A conscious effort was made during data collection to taxonomically identify each specimen without *a priori* assumptions regarding previous researchers' assignment of species. These identifications were made visually based on the criteria outlined in Table 4.2. Taxonomic assignments made on visual assessment 'in the field' were removed for the potential *A. australis* specimens listed in Table 6.20 '*Antidorcas* results' section 2, to remove any potential bias based on prior taxonomic assumptions.

Scatter plots of all fossil species and modern springbok were made, comparing BLW (bucco-lingual width) against MDL (mesio-distal length) (see Figure 6.3-Figure 6.8) to assess dental occlusal area in *Antidorcas*. Subsequently, scatter plots were made using enamel thickness data (see Figure 9.2). Discriminant function analyses were then applied to see if the morphology of any of the '*A. australis*' specimens aligned with known *A. recki*, *A. bondi* or *A. marsupialis* (fossil and modern) (Figure 6.13). Finally, evidence from dietary methods (use-wear and isotopes) was applied.

4.3 Linear Morphological Measurements Method

Basic dental measurements were taken of selected *Antidorcas* specimens from each member (Figure 4.14). Where present in an assemblage (i.e. where present and full measurements were obtainable, and not limited by damage), a maximum of 30 teeth from each species for each member were selected. Permanent second molars were preferentially selected as the methods used here to obtain palaeodietary information can be implemented ubiquitously. If M2s were not in sufficient abundance for any particular species or member, measurements were taken additionally for permanent first and/or third molars. Maxillary (upper) and mandibular (lower) molars were analysed separately for all measurements [i.e. All M_1s together, separated from all M^1s, All M_2s together, separated from M^2s, All M_3s together, separated from M^3s.]. A total of 704 *Antidorcas* dental measurements were obtained (181 Modern and 523 fossil). Maxillary second molars (M^2) were shown to be the most abundant in the fossil record and were primarily used for analysis, giving a total of 361 *Antidorcas* measurements (64 modern and 297 fossil). M_2 were secondarily used. M1 and M3 (maxillary and mandibular dentition separated), were also analysed (separately) for corroborative purposes.

Descriptive statistics for second molars are summarised in *Antidorcas* results chapter tables (Chapter 6,Table 6.1-Table 6.5). Corresponding tables for first and third molars are included in the appendices (Appendix A6).

A selection of modern *Antidorcas marsupialis* dentition were measured for comparative purposes and to establish expected levels of intra-specific variation. All permanent molars were measured for each individual. As the most abundant tooth type from the fossil sample was selected for primary analyses (M2), the corresponding tooth type is selected from the modern dataset. Where an individual yielded more than one set of measurements (i.e. left M^2 and right M^2), both measurement sets were taken through to analysis. This was to ensure comparability with the fossil dataset as there is no reliable way to identify isolated molars to individuals in an assemblage and there is the possibility of taking more than one molar (both left and right M^2) from an individual as part of the fossil dataset.

Each molar was assessed using Rautenbach's (1971) ageing criteria and given a wear rating. Very young or unworn dentition, and old or very worn dentition was excluded from analyses to avoid influences of age and wear level as far as possible (this is primarily of importance for enamel thickness measurements).

Modern *A. marsupialis* and supplementary species (*Damaliscus pygargus* and *Tragelaphus strepsiceros*) were subjected to the same metrical analysis to establish the likely intraspecific variation parameters and anticipated levels of change and variability through time. Enamel thickness measurements were taken for modern *A. marsupialis* only (not for supplementary species). Enamel thickness was measured on all molars across the toothrow for upper and lower dentition. In line with the other measurements and due to the variation in enamel thickness across the toothrow, and between upper and lower dentition (Winkler and Kaiser 2015), each molar type is analysed separately.

Data was sorted and preliminary descriptive statistics calculated in Excel v.1804. All statistical analyses were completed in SPSS. Data was tested for normality prior to

statistical analysis to accurately subject data to either parametric or non-parametric analyses. All measurements were subject to an independent samples Kruskal-Wallis Test and post-hoc Mann-Whitney U pairwise comparisons, with Bonferroni adjusted significance levels.

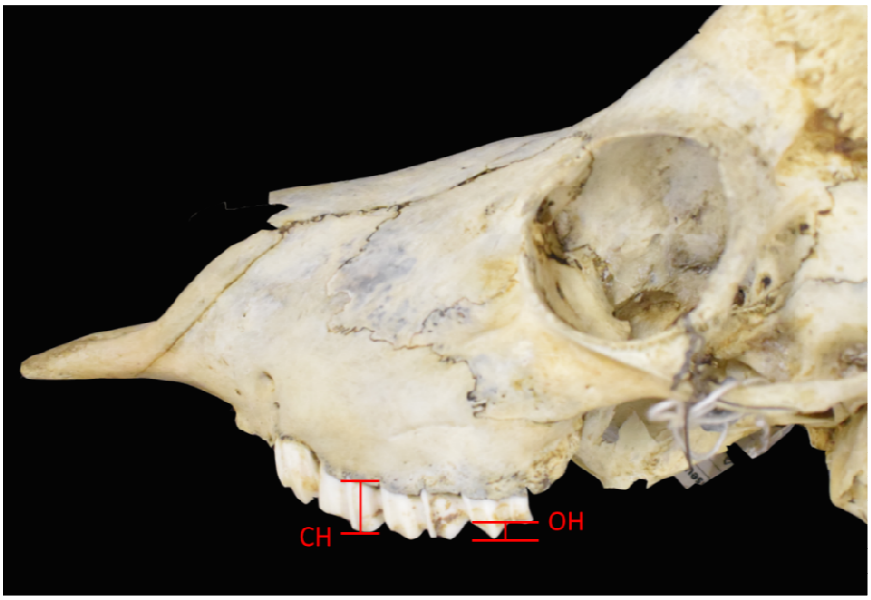
Glossary of dental and measurement terms used:

Maxillary M2 = UM2 or M^2
Mandibular M2= lm2, LM2 or M_2
Right upper second molar: RUM2 / RM^2
Left lower second molar: LLM2 / lm_2

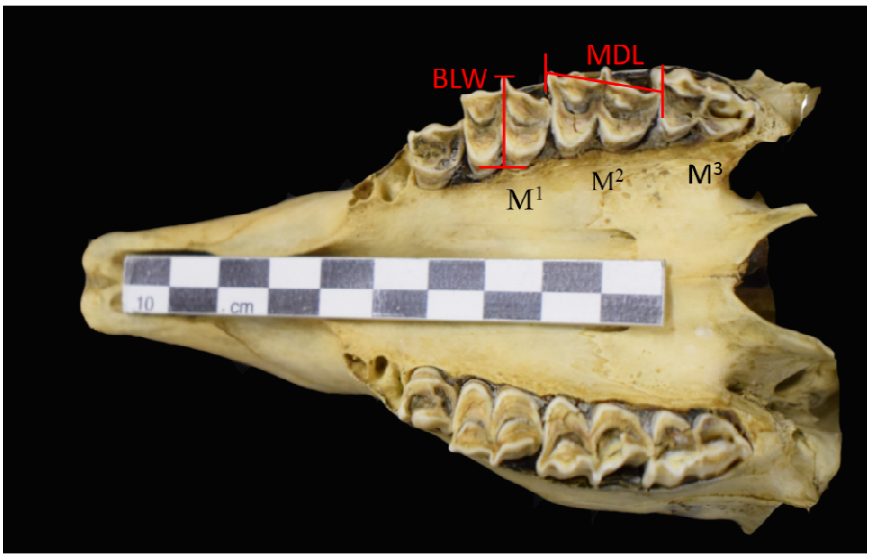
Dental molar measurements taken:

BLW: Bucco-lingual width
MDL: Mesio-distal length
OH: Occlusal Height (cusp height)
CH: Crown Height (in situ dentition)
TH: Total Height (of isolated molars)
Enamel Thickness (A, B, C, D)

A



B



C

Figure 4.14: Measurements taken of each tooth and tooth position. Images [A, B] of Antidorcas marsupialis (TM 13232) maxillary plate with location of measurements taken for each tooth. and [C] isolated tooth (SK 2366). Scale bar represents 10mm.

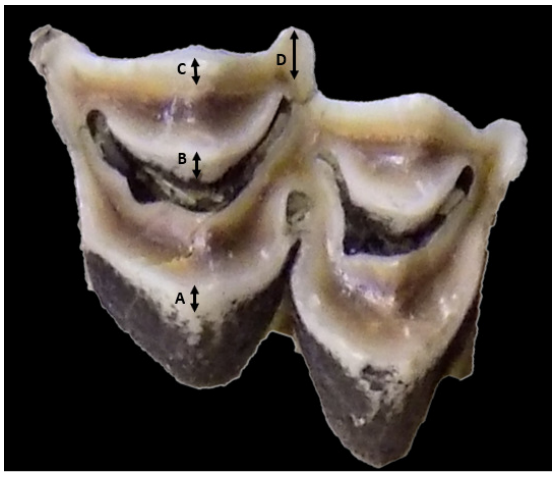
4.3.1 Enamel Thickness Measurements

Enamel thickness has been linked to dietary abrasiveness (e.g. Damuth & Janis 2011; Janis & Fortelius 1988, Martin 1985). Investigating the differences and changes in enamel thickness is implemented here with the intention of achieving insight on the likely abrasiveness of *Antidorcas* diets, which may manifest as increased dental enamel thickness as an ancestral and/ or adaptive (if consistent increase/ decrease occurs through time) trait.

Enamel thickness may also have been altered by taphonomic processes, yet it is envisaged that taphonomy would act relatively consistently, irrespective of species, within the same deposit and therefore any differences can be inferred to be predominantly reflective of those present in the living assemblage.

The thickness of the dental enamel has the potential to impact on the isotopic values obtainable if only the outer enamel layers are taken for sampling due to the enamel mineralisation process (Reade et al. 2015).

1



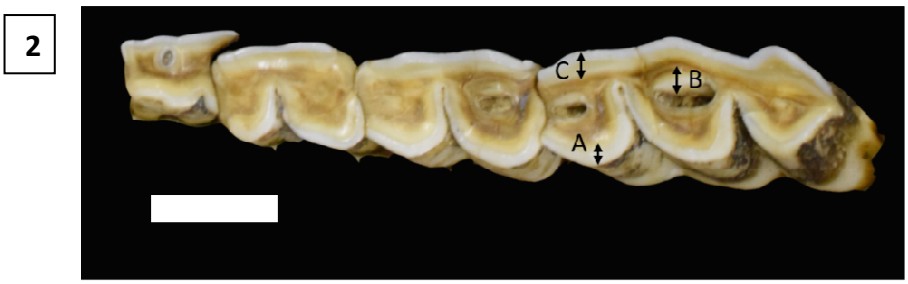


Figure 4.15: Location of enamel thickness measurements taken on upper molars (1) and lower molars (2). Location point 'D' (thickness of mesostyle) is not present on lower molars.

Table 4.3: Locations of measurements taken on dental molars

Location	**Maxillary**	**Mandibular**
A	Lingual enamel band [protocone/ hypocone]	Buccal enamel band [protoconid/hypoconid/hypoconulid]
B	Internal enamel band [Paracone/ metacone]	Internal enamel band [metaconid/entoconid]
C	Buccal enamel band	Lingual enamel band
D	Mesostyle	Not present

Table 4.3 and Figure 4.15 show the locations from which enamel thickness measurements were taken on the tooth. The difference between upper and lower dentition is visually represented here, whereby lower molars enamel thickness A is located on the buccal enamel surface and thus has different masticatory pressures exerted to the maxillary enamel thickness A location (located on the lingual enamel surface). These two locations may be subject to differing abrasiveness from vegetation in the palette according to the masticatory movement of the jaw, the precise detail of which tends to be species specific.

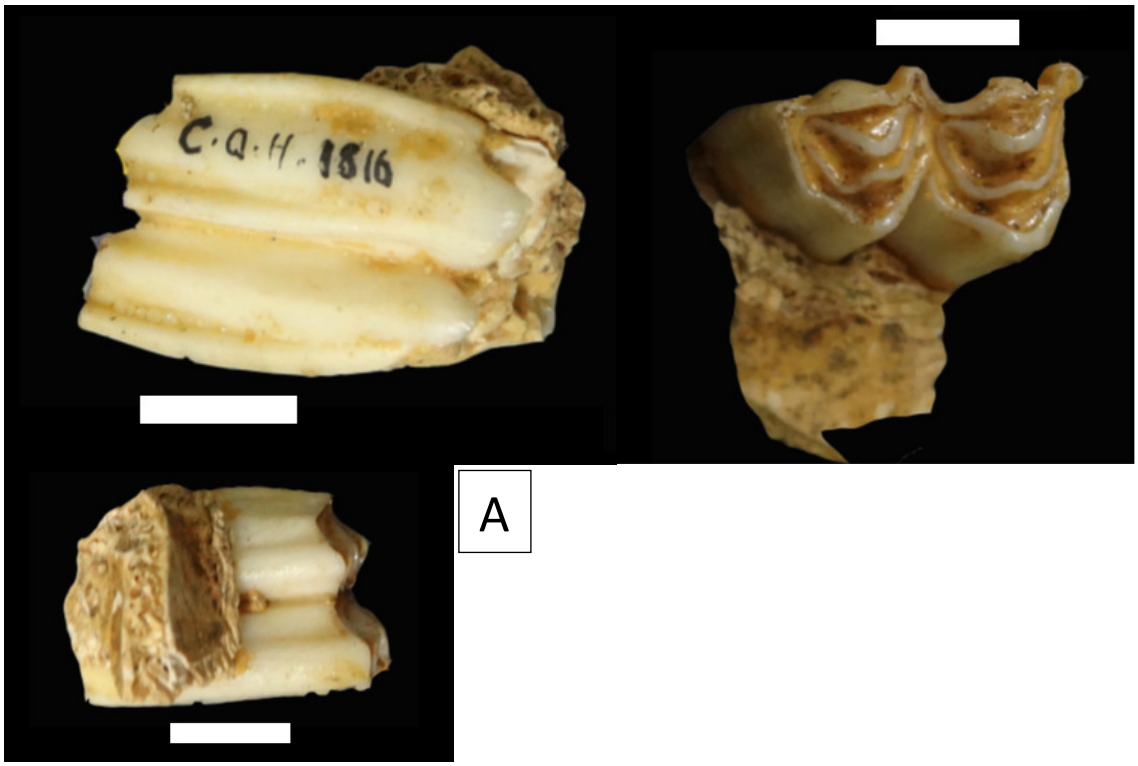
It is acknowledged that some level of variation may arise from obtaining measurements from slightly varying points. However, every effort was made to ensure all measurements were taken at the same point on the tooth. Measurements are taken at the point of typical maximum enamel thickness along the relevant facet. Further research (beyond the scope of this study) into the exact morphology of dental shape and enamel thickness would be of benefit to scrutinise morphological variation more closely.

4.3.2 Considerations

Taxonomic identification As discussed, identifying to species level from isolated molars presents challenges. For example, S94-8283 from Sterkfontein Member 5 West had been identified as 'Antelopini'. This taxonomic identification was originally assumed here. However, this is definitely not *Antidorcas* as it is too large and morphologically dissimilar to the *Antidorcas* dentition. Other African Antelopini species include: gazelles, gerenuk and blackbuck. Grant's gazelle or similar is the only possible size candidate when considering modern body size of extant species. Alternatively, it belonged to a now extinct form of Antelopini or, another tribe altogether. As refined species identification as possible is crucial, with only millimetres of morphological differences separating species and genera, to ensure accuracy when attempting to pick up on any morphological changes at species or genus level through time.

Intra-specific variation Difficulties may arise in anticipating the levels of intra-specific dental variation in fossil species. Further, which specific features one should anticipate

higher levels of variation in than others, may be changeable. For example, COH 1816 (Figure 4.16) looks more morphologically similar to *Aepyceros melampus* (the impala) than to *Antidorcas*. Yet as Vrba's (1973) identification of *A. bondi* makes clear, there are a plethora of similarities between *Antidorcas bondi* and *Aepyceros melampus*.



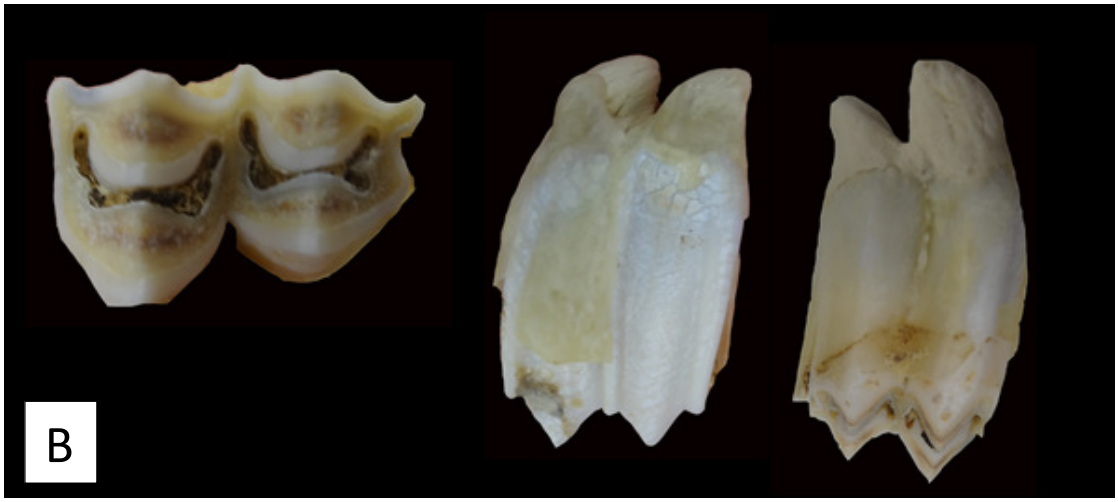


Figure 4.16: Images of A) COH 1816, 'Antidorcas' upper molar identified from cave of Hearths and comparative modern B) A. melampus (NMS Z. 20002.212.5) and C) A. marsupialis (NMS 2002.212.2) all in buccal, occlusal and lingual view.

Overlap of species It is probable that there will be morphological similarities and dimensional overlap between *Antidorcas* species. For example, between large females of *A. recki* and small males of *A. marsupialis*. This is an issue when attempting to identify lineage changes and major evolutionary events (i.e. speciation) from consistent morphological directional changes (e.g. a noticeable prolonged enlargement of the bucco-lingual width of an *Antidorcas* species or sustained hypsodonty increase). This is mitigated by extensive consideration of species based on features other than linear measurements (see 'Taxonomic identification of *Antidorcas* species' sections and chapter 6, section 2), allowing for intra-specific changes through time to be noticeable.

When *Antidorcas* (as a genus) measurements through time are used (although identified individually to species), the trend through time is likely to prevail for the genus, to at least be able to identify change at the general level. I.e. unless direct character displacement creates opposing selection pressures, an increase in grazing through time is likely to select for increased crown height, which should be reflected at the genus level.

Identification of tooth-type Molar-averaging is likely to occur (i.e. a combined signal from all molars). For the majority of techniques implemented, this does not cause a major issue. However, when attempting to understand the nature of *Antidorcas* dental evolution from a morphological point of view, size and shape averaging across the molar row can confuse the signal. For example, SK 41626 is a left maxillary molar with similarities to M1 in the roundedness of the lingual cusps but the extended posterior style characteristic of an M3. This specimen was treated in analysis as an M3. To ensure accuracy, initial identifications of tooth types were corroborated by published sources where possible and from photographs taken of each specimen.

4.4 Mesowear Methods

All specimens selected for dental measurements were subject to mesowear analysis, providing their cusps were intact. Providing juvenile and heavily worn teeth are excluded, age-related wear stages do not infringe upon mesowear values. Traditional mesowear variables include occlusal relief, cusp shape and a combination of these factors to create a 'mesowear score'. These variables are used in this research, scored following Figure 4.17 below. The method is then developed further for this study as detailed later in this chapter.

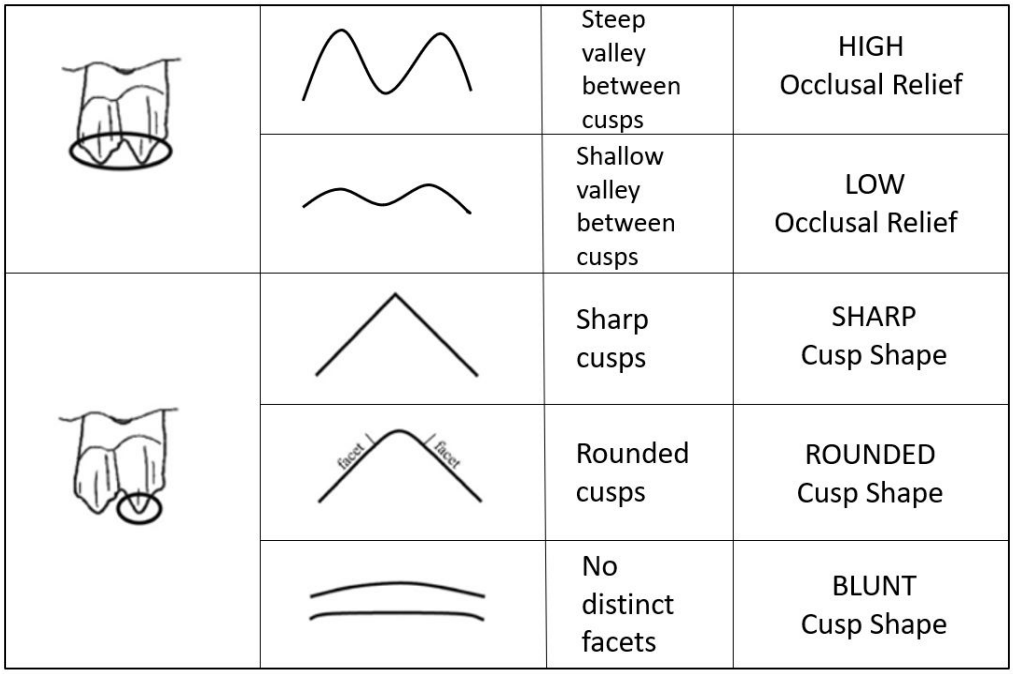


Figure 4.17: Mesowear scoring parameters defined by Fortelius and Solounias 2000 (Figure from Sewell et al. 2019 p. 6, Figure 2).

The four main dietary categories obtainable from mesowear variables identified by Fortelius and Solounias (2000) are: grazer, grazing-dominated mixed feeder, browse-dominated mixed feeder and browser; going from abrasion-dominated to attrition-dominated respectively. Cusp shape and relief are not entirely independent variables as the progressive blunting of tooth cusps inevitably reduces dental occlusal relief (Fortelius and Solounias 2000), as such, mesowear scoring systems (from LB [low relief, blunt cusps] to HS [high relief, sharp cusps] or vice versa) have been established (e.g.Fortelius and Solounias 2000; Kaiser and Schulz 2006; Louys et al 2012; Kubo and Yamada 2014; Croft and Weinstein 2008). Certain wear patterns are less likely to occur, High relief, blunt cusps, for example, would be rare to see and has been excluded in some publications (e.g. Kaiser et al. 2009's '0-4' scoring method).

Modern specimens were assessed for significant differences to establish expected fossil intra- (*Antidorcas* sub-species comparisons) and inter-specific (comparisons between *Antidorcas*, *Damaliscus* and *Tragelaphus*) ranges of variation for each dietary category (grazer, browser and mixed-feeder). Where more than one tooth from the toothrow was scored on the same individual, all scores were included. This is to ensure comparison with the fossil collection, which could comprise of dentition from the same individual, represented by multiple isolated molars.

Mesowear as a Dietary Indicator

Both the mechanical properties of mastication and of the food itself can impact upon mesowear gradients (Janis 1990). Tooth morphology is determined by a combination of ancestral traits (dental structure and phylogenetic history) and dietary input (e.g. Janis 1988, 1995; Damuth and Janis 2011). Mesowear is a methodology similarly derived from the observations of tooth morphology, occlusal height (relief) and profile (cusp shape). Occlusal contact (tooth-tooth) produces characteristic attritional wear patterns (Butler 1952), these wear patterns can be used to deduce directions of jaw movement during mastication and the lifetime diet of the individual.

Fortelius and Solounias (2000) pioneered this macro-level dental use-wear method for determining the diet of ungulates. Based on relative facet development, mesowear is used to differentiate between feeding types (along a grazing to browsing spectrum) and by inference, allow an informed palaeovegetational signal for the respective temporal and geographical range (Blondel et al. 2010; Kaiser et al. 2013).

Abrasive particles in masticated foodstuffs cause additional, abrasive wear (food-tooth). It is the combination of abrasive and attritional wear that results in the mesowear patterning evident in herbivore dentition. Attritional contact creates facets, resulting in high relief between cusps and sharp cusp apices. Conversely, abrasive food-tooth contact obliterates dental facets, thereby reducing the depth between cusps and producing rounded apices (Fortelius and Solounias 2000; Kaiser et al. 2009). Highly abrasive diets, such as is typical of grazers (but see Janis 1995; Damuth and Janis 2011) lead to greater wear of the occlusal surface, resulting in lowered occlusal relief and rounded/ blunted molar cusps (Fortelius and Solounias 2000). Browsers tend to have higher occlusal relief and sharper cusps than grazers (Chapter 4,

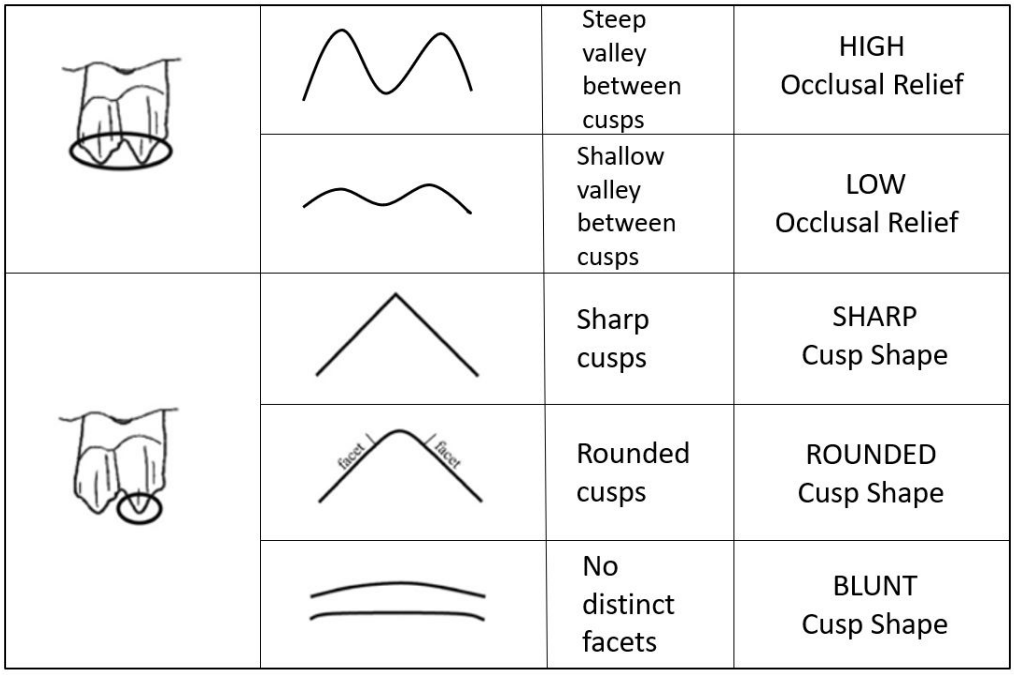


Figure 4.17; Kaiser and Fortelius 2003). No extant grazer has more than 40% (of a species' population) sharp cusps and no extant browser has more than 10% blunt cusps (Fortelius and Solounias 2000). Mixed feeders may show no significant differences from browsers

(Fortelius and Solounias 2000), suggesting browse has more macroscopic impact on wear. This is also likely for microscopic wear, with browse particle-induced wear likely to be sustained for longer (see 'DMTA' section).

A general relationship between climatic factors (e.g. humidity) and the properties of the vegetation available is likely. The abrasiveness of certain foods can also vary depending on the part of the plant consumed and the quantity (Kaiser and Schulz 2006). Low quality grasses, of which a considerable amount needs to be consumed in order to maintain nutritional needs, induce considerable abrasion on the dentition, thus grazers tend to have blunter cusps.

Considering the dominant diets of *Antidorcas* for each discrete temporal period (member) [based on mesowear values for *Antidorcas* in each members' assemblage], inferences can be made in relation to the overall vegetation cover and trends from the surrounding temporal periods. Establishing intra- and inter-specific mesowear ranges within each *Antidorcas* assemblage provides insight into the homogeneity of dietary preferences and by inference, of vegetation cover.

Regional and seasonal dietary variations can be implied via the individual ranges of mesowear patterns within the population/ assemblage (e.g. Kubo and Yamada 2014). Combined with the phylogenetic adaptations (e.g. crown height) addressed previously, the added mesowear values will shed light on the diet of the individual animals and contribute to knowledge of the dietary preferences of the *Antidorcas* species.

Mesowear and Dietary Abrasiveness

Rounding or blunting of molar cusps may be due to abrasive silicas found in grasses, or other abrasive agents. Before concluding a dietary category for each species/ individual animal, each method can be assessed alongside the lifetime wear patterning provided by mesowear to give a more holistic insight into feeding and habitat preferences. For example, Sanson et al's (2017) study based on African buffalo (*Syncerus caffer*) in the Kruger National Park, examining the relative contribution of exogenous (dust/grit) and endogenous (plant silica) particles to tooth wear, proposed an interaction between these abrasives (endogenous and exogenous particles) and suggest that abrasion should be considered more holistically. That is, rather than simply exerted via a grazing or a browsing -type diet.

In this way, mesowear can provide an indication of potential selective pressures acting upon *Antidorcas*. Feedback systems within the dentition may act in response to the presence of particles during chewing, to reduce the occlusal load and therefore, reduce excessive damage (Lucas 2004). The cumulative impact of such feeding would likely result in dental evolution towards greater crown height or other similar reinforcements, as found by Hummel et al. (2010; see 'measurements' chapter, chapter 7).

Mesowear as a Palaeovegetation Indicator

Due to the properties discussed above, mesowear can be indirectly indicative of the spread of grassland. The abrasiveness of a grazing diet will result in herbivores with flatter (more abraded) molars. Theoretically, the expected evolutionary transition from browsing to grazing would show in the dentition of ungulates, with a transition from low to high crowns

(Janis 1988; Janis and Fortelius 1988; Solounias and Semprebon 2002) with decreased relative cusp heights.

Choice of habitat and feeding style have been shown to be as important as diet in determining levels of hypsodonty (as discussed in chapter 7) due to the inclusion of dust/grit on low level vegetation in dry environments (e.g. Janis 1995). The level of hypsodonty can therefore be seen as the long-term selective pressure of a feeding behaviour that would produce heavy and abrasive wear on a mesowear scale (i.e. preference of low occlusal relief and rounded to blunted cusps) (but see Mihlbachler and Solounias 2006).

Mesowear has been utilised previously to indicate climatically-driven environmental parameters, related to humidity and seasonality. The attrition/abrasion mesowear equilibrium can reflect climate driven habitat conditions. High dental occlusal reliefs and rounded cusps are positively correlated with mean annual precipitation, water balance and humidity; which may be complemented by oxygen isotope analysis (see chapter 10 'Stable isotope analysis'). Low relief, blunt cusps are negatively correlated and are restricted to drier environmental conditions, where more dust and particulate matter is incorporated on plants, resulting in higher incidences of abrasive wear (Kaiser and Schulz, 2006). Climate-driven vegetational gradients cause a shift in the mesowear equilibrium independent from species-specific dietary adaptations (Kaiser and Schulz 2006).

Developing the Method Further

Mesowear is inexpensive and can be done relatively quickly, providing an overview of faunal diet (Loffredo and DeSantis 2014; Jones and DeSantis 2017). However, it is highly subjective, and scoring can vary considerably depending on a plethora of issues, such as the selection of specimens being observed at any one time, when breaks were taken, lighting and so on, rendering scores relatively incomparable between observers and between studies. Due to the hereditary element of molar morphology, inter-specific differences can be masked. For instance, the majority of variation for the *Antidorcas* appears to be above 'low' threshold when considering only *Antidorcas*. A lot of variation in size and cusp height just fall into the 'high' relief category with no further distinction available. Yet when compared to other species, *Antidorcas* appears to typically have low relief (see new mesowear categories, Table 4.4).

Moreover, the determining factors behind mesowear scores are not necessarily as clear-cut as suggested. When dealing with extinct species it can be difficult to ascertain the causes of observed physical characteristics. A certain degree of the appearance of the teeth could be due to post-depositional processes (taphonomy, explosion or excavation processes). There is the potential that other factors also impact the physical properties of the dentition. For example, the impact of grit and dust ingested on mesowear is not fully known. Understanding its impact could enlighten on other environmental aspects.

Differential mesowear across the tooth

Many of the third molars in this study show differential wear on the facets on the same tooth, which could easily be scored in three different categories. This is presumably due to the function of the tooth in mastication, with the facets being differentially exposed to abrasive food particles or being in contact with the opposing dentition (attritional wear).

For example (Figure 4.18; fossil *Antidorcas* left M_3 COH 1543). Fortelius and Solounias (2000) identify this occuring and classify individuals where this occurs as 'mixed cusps'- for either inter or intra-tooth variation. Simply scoring the sharpest cusp, as is often practiced (e.g. Fortelius and Solounias 2000), may cloud the palaeovegetation signal obtainable (DeSantis et al. 2018).

Figure 4.18: Fossil Antidorcas left M_3 COH 1543 showing differential mesowear appearances across the facets on the same molar. Scale bar represents 10mm.

Traditional methods would score only the sharpest cusp on the upper second molar (Fortelius and Solounias 2000). However, when extending the method to fossil bovids, where tooth type and taphonomy may not allow sufficient sample size of the preferred molar (M^2), advancements in the method and decisions on the mesowear values represented by molars such as these (Figure 4.18) are valuable.

Testing the mesowear method

Due to the many considerations, the method was refined for this specific dataset. Further, because of the apparent subjectivity and confounding factors surrounding mesowear, experiments to assess the reliability of this method were conducted, to look for the source of error in dietary and palaeoenvironment signal discrepancies found from the fossil analysis. Two small experiments were conducted to test the merit of using the traditional mesowear methodology established for the field (Fortelius and Solounias 2000) and the viability of using photographs of specimens to assign scores (with the aim of reducing travel costs and creating an online database of specimens to increase access for researchers). These experiments were conducted as part of this research, and help to inform on the reliability and limitations of the mesowear method but do not assist in answering the fundamental research questions of southern African palaeoenvironments. Therefore, the experiment is detailed in full in Appendices A7 but not discussed further in the central body of the thesis.

4.4.1 Refining the Method for Mixed Feeding Bovids

From results of the experiments (Appendix A7), extra categories to allow refinement of mesowear scoring for this dataset were introduced.

New Mesowear Categories:

Table 4.4 details the categories trialled in this research. The first letter (for both occlusal height and then for cusp shape) shows the dominant category. For example, molars displaying obviously low occlusal relief with blunt cusps are scored as 'LB'. Where there is some difficulty in assigning between high/low relief, the dominant category is chosen as the

first letter, so ‘L-M’ (low to medium) shows lower relief than ‘M-L’ (medium to low). If there is no definitively dominant category, ‘M’ is chosen. The same logic is used for cusp shape.

For initial multivariate statistical analysis, relief scores are assigned based on the closest assignment. Original mesowear scores were given as high or low relief (2016 data collection). To ensure consistency, those given new mesowear scores, including medium relief (from 2017 data collection), are also given a separate high/low assignment. Where the new mesowear score is ‘H-M’ (high to medium) or ‘M-H’ (medium to high) (the first letter is the dominant category but is not as clear as if scored as only ‘H’ (high) or ‘M’ (medium)), the tooth is assigned high relief. If the new mesowear score is ‘L-M’or ‘M-L’, the tooth is assigned low relief. Where the relief has been said to be ‘M’, photographs of the specimens were used to assign either high or low relief for this purpose.

Additional Mesowear Scoring Method Implemented in This Research:

Rautenbach’s (1971) ageing criteria of the springbok was used to assess age and wear rates, in order to eliminate very old (and very worn) or very young (unworn) molars. This is to mitigate for the impact of age-wear on mesowear variable scores as far as possible (although challenging for isolated teeth, without the toothrow to more accurately assess wear).

Upper molars were scored from the buccal view, lower molars from the lingual view, according to

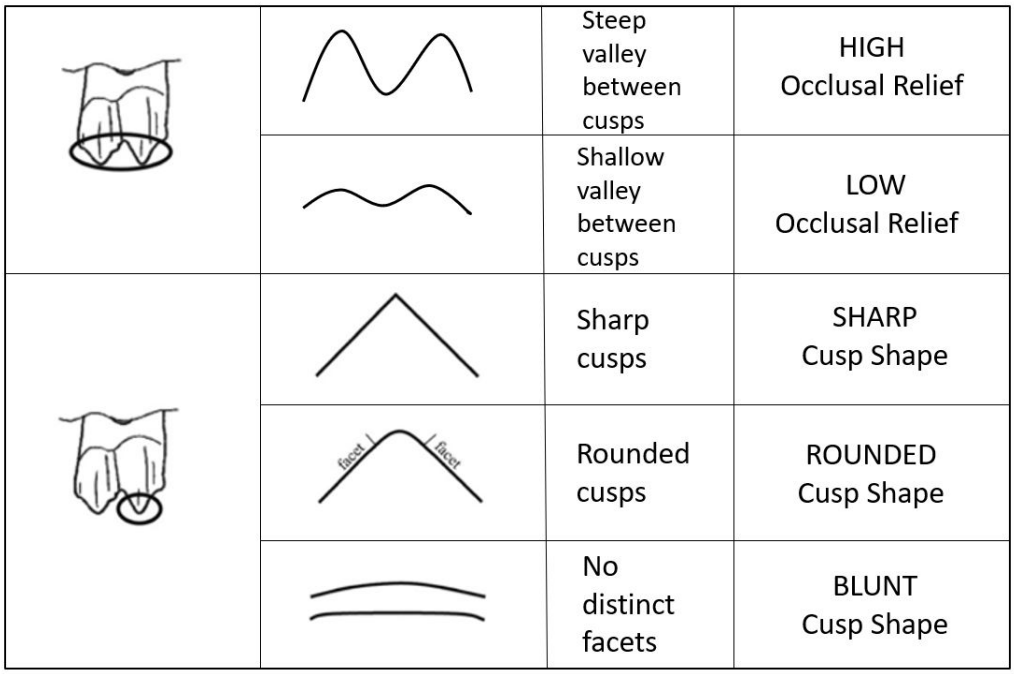


Figure 4.17, with ‘medium’ relief scored if it was between high and low relief. Upper and lower dentition are analysed separately to ensure comparability (e.g. Fortelius and Solounias 2000; Blondel et al. 2010; Loffredo and DeSantis 2014). Mandibular dentition is believed to be more likely to emphasise the grazing proportion of a diet due to lower molars having a tendency towards flattening (e.g. Fortelius and Solounias 2000).

Table 4.4: New mesowear scoring categories trialled in this research; a continuous scoring scale for mesowear. Scores are given according to occlusal relief alongside cusp shape, viewed from the buccal view of maxillary molars and the lingual view of mandibular molars.

LB	1	**L-MB**	8	**M-LB**	15	**MB**	22	**M-HB**	29	**H-MB**	36	**HB**	43
LB-R	2	**L-MB-R**	9	**M-LB-R**	16	**MB-R**	23	**M-HB-R**	30	**H-MB-R**	37	**HB-R**	44
LR-B	3	**L-MR-B**	10	**M-LR-B**	17	**MR-B**	24	**M-HR-B**	31	**H-MR-B**	38	**HR-B**	45
LR	4	**L-MR**	11	**M-LR**	18	**MR**	25	**M-HR**	32	**H-MR**	39	**HR**	46
LR-S	5	**L-MR-S**	12	**M-LR-S**	19	**MR-S**	26	**M-HR-S**	33	**H-MR-S**	40	**HR-S**	47
LS-R	6	**L-MS-R**	13	**M-LS-R**	20	**MS-R**	27	**M-HS-R**	34	**H-MS-R**	41	**HS-R**	48
LS	7	**L-MS**	14	**M-LS**	21	**MS**	28	**M-HS**	35	**H-MS**	42	**HS**	49

KEY
L-low relief
M-medium relief
H-high relief
B-blunt cusps
R-rounded cusps
S-sharp cusps

The following variables were assessed for each tooth:

- Relief: high or low relief
- Relief: high, low or medium relief
- Cusp shape: Sharp, rounded or blunt
- Mesowear scores: 0-4 (Kaiser et al. 2009) and 1-6 [1=LB, 2=LR, 3=LS, 4=HB, 5=HR, 6=HS].
- New mesowear categories were implemented and trialled for this research, [1(LB) – 49 (HS)], see Table 4.4.
- Mesowear III scores (Solounias et al. 2014) on the internal enamel band, on upper molars only.

Antidorcas and supplementary species permanent molars were scored 'in the field' and corroborated from photographs taken at the time of the original scores. Some duplicates were made of selected mesowear scores from 2016 to 2017 data collection trips. Following from preliminary results, obtained via data collection in 2016, sample sizes were significantly increased to investigate potential patterns (Sewell et al. 2019) further. All scoring was undertaken personally, without looking at previous scoring. In spite of a consistent photography protocol, unavoidable minute angle changes and light differences could alter perceptions of occlusal relief and cusp shape. Photographs, although unreliable for definitive mesowear scores when used in isolation, were beneficial for confirming visual mesowear assessment when away from the dental specimens. Photographs were used for corroboration where discrepancies between variables exist (e.g. 2016 score of high relief, sharp cusps and 2017 score of low relief, rounded cusps for the same specimen). Where repeated scoring yielded differing results, photographs taken in 2016 (by Rupert Cope and L. Sewell) and 2017 (by Lucile Crété and L.Sewell) were used to establish the most appropriate mesowear values. Moreover, where discrepancies occurred, the sharper mesowear values (relief, cusp shape and score) were selected, as bluntness is more likely to be a taphonomic artefact (Franz-Odendaal and Kaiser 2003).

4.4.2 Mesowear III

Solounias et al. (2014) described and tested a new method of mesowear, termed 'Mesowear III', with focus on specific facets, namely the metacone and paracone. This uses the same facets as used in DMTA, thereby allowing some degree of comparability between the methods. Therefore, an attempt to implement this method was made in 2017. Although some mesowear III scores were obtained, this method does not form a central part of this research due to small sample sizes. Only upper molars can be used for this method, reducing potential sample sizes. Additionally, many of the specimens used here showed taphonomic wear on the relevant facets, further reducing sample size. Although a relatively novel method, Mesowear III or 'inner mesowear' scores have already been successfully implemented on Middle Pleistocene ungulates, establishing fossil palaeoecology (Strani et al. 2018) and would be of benefit to relate to inner enamel thickness (location B) measurements (see 'measurements' method above). Mesowear III sores when separated by species and provenance sample sizes are too small to show any significant differences and are only analysed by species and through time (for all *Antidorcas* specimens combined).

Analysis Method:

Modern *Antidorcas* is analysed initially to establish the best method of analysis and combination of results to take forward for the fossil samples. That is, considering which samples could be grouped together to enable larger sample sizes whilst maintaining accuracy (without potentially falsely averaging across the toothrow, for example).

Basic descriptive statistics are calculated showing the number of specimens falling in each mesowear category and their relative percentages calculated. All statistics are analysed in SPSS v.23/24. Medians are calculated to allow comparisons between each ordinal mesowear variable within each category. Independent samples kruskal-wallis test with post-hoc Mann-Whitney U pair-wise comparisons are conducted to test for significant differences between members intra- and inter-specifically (*Antidorcas,* and supplementary species (separately analysed)).

Finally, data reduction via a principal component analysis (PCA) and discriminant function analysis (DFA) is carried out on the mesowear variables of all *Antidorcas* species. *Antidorcas* as a genus and individual *Antidorcas* species mesowear trends through time are evaluated.

4.5 DMTA

Sampling Strategy

Permanent molars were selected for microwear analysis based on the completeness of their occlusal surface. If the facets of interest (Figure 4.20-Figure 4.21) were complete, molars were separated for potential analysis. Of these selected specimens, a maximum of 20 specimens per *Antidorcas* species (*recki*, *bondi* and *marsupialis*, where present) per site (or 10 of each of the supplementary species) were chosen for microwear analysis.

Modern *Antidorcas marsupialis* from National Museums Scotland, Edinburgh (n=3), Natural History Museum, London (n=25) and the Ditsong Museum of Natural History (n=10) were cast to establish the modern mixed-feeding DMTA signal and assess the anticipated dietary parameters for fossil *Antidorcas*. Modern *Damaliscus pygargus* (n=10) were used to establish expected grazing signals.

Data was supplemented with modern DMTA data for species with known diets, *Alcelaphus buselaphus*, *Syncerus caffer*, *Cephalophus sylvicultor* and *Giraffa Camelopardalis*. This data, cited here for comparative purposes, belong to Dr Gildas Merceron, Laboratoire de Paléontologie, Évolution, Paléoécosystèmes, Paléoprimatologie (PALEVOPRIM; ex-iPHEP), Université de Poitiers.

Antidorcas specimens are used at genus level initially to assess palaeovegetation change through time. They are then separated to species level to establish *Antidorcas* palaeoecology for each species and any changes therein through time.

Individuals are selected at random to assess the impact of individual variation on the overall microwear signal for any given member (Provenance). A group of individuals are also used to examine how species and individual preference influences the palaoevegetation signal obtainable. For this, the '*A. australis*' subset is used here (see 'Taxonomic Identification of *Antidorcas* species'). This subset is used as it may contain any *Antidorcas* species and is

represented in the focus members for the main sites (Sterkfontein, Kromdraai and Swartkrans).

Microwear as a dietary indicator

From microscopic wear patterns, animals' diets can be categorized into distinct feeding groups. Although an oversimplification and new categories have since been added, Hoffmann and Stewart's (1972) distinctions of grazing, browsing and mixed feeding, can be used to identify a herbivore's diet, which can subsequently be used to infer the nature of the vegetation cover of the landscape that that species inhabits (or inhabited).

When examining images produced through DMTA (alternatively known as DASTA), grazers have higher epLsar values, showing more anisotropic microwear surface textures, whereas browsers have higher Asfc values, indicative of more complex microwear surface textures (Ungar et al. 2007). Going beyond simple grazing versus browsing insights, leaf browsing for example, produces anisotropic surfaces (high Asfc) with high homogeneity (low HAsfc) via uniform pits. The opposite signal is obtained from fruit browsers. As such, DMTA enables a more holistic view of an animal's palaeoecology.

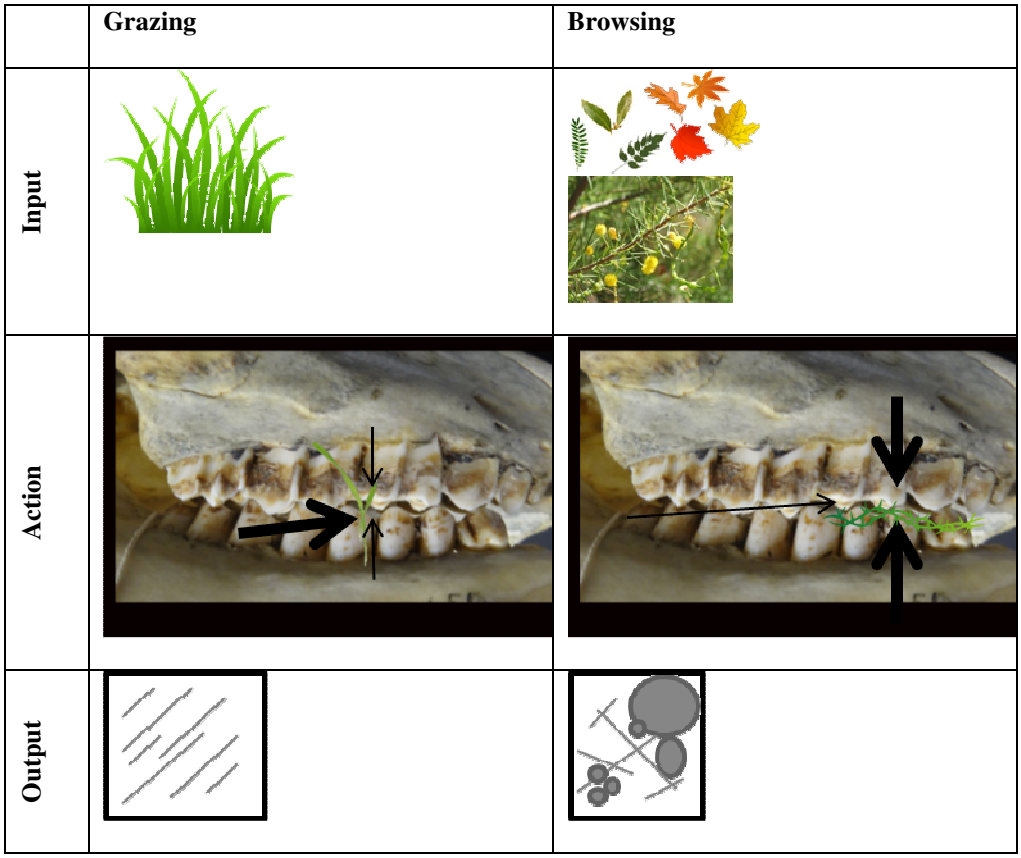


Figure 4.19: A simplified representation of how microwear is impacted on dental enamel surfaces differentially, according to diet. Bold arrows indicate the strongest forces acting on the dental enamel surface. When grazing, phytoliths (plant stones) within grasses are dragged across the surface of the tooth, causing striations in a uniform direction. When browsing, the main force exerted is the downward pressure between the upper and lower teeth onto the browse substance, creating pits into the enamel (of varying sizes).

Grazers feed predominantly on monocotyledons (e.g. grasses) and browsers (e.g. trees and cacti) on dicotyledons (Merceron and Ungar 2005). The microwear patterns are produced because of the differing physical properties and nutrient contents of grasses and browse (Shipley 1999; Solounias and Semprebon 2002; Schulz et al. 2013a).

Scratches are believed to be caused by hard (typically grass silica bodies, i.e. phytoliths) particles being dragged across the tooth surface in a uniform manner, usually directed labio-lingually (Schubert et al. 2006) during the shearing phase of mastication (Baker et al. 1959; Ungar et al. 2007). Browse does not contain as high a concentration of phytoliths as grasses do, and the phytoliths present tend to be smaller (McNaughton et al. 1985).

Contrastingly, pits are caused by indentation into the enamel from the vertical force of the upper and lower dentition closing onto the food particle (typically from browse-type materials such as twigs/seeds) (Solounias and Semprebon 2002; see Figure 4.19). Browse vegetation is typically harder, or more brittle, requiring crushing, which leads to pit formation. Pits can be formed by a variety of particles and actions and understanding the aetiologies of pit formation allows informative inferences about diet to be made. The size and shape of each pit is dependent on the particle that caused it (e.g. Lucas et al. 2014). The prevailing belief is that larger pits are caused by concentrated pressure on hard food between enamel surfaces, leading to puncture crushing. In contrast, smaller pits tend to be formed by tooth-to-tooth wear (Teaford and Runestad 1992).

Due to the abrasiveness of a grazing diet, where food particles are continually dragged across the tooth surface during mastication, at a relatively shallow depth into the enamel surface, microscopic wear on the enamel surface gets overwritten more regularly than occurs from the less abrasive practice of browsing, that creates pits at a relatively greater depth into the enamel surface.

Interestingly, Solounias and Semprebon (2002) identified a differentiation in scratch appearance based on the properties of the grass eaten. Isotopic analysis will show the differential levels of C_3 to C_4 grasses in the diet (see chapter 10 'Isotope analysis'). Coarse scratches were shown to be typical of C_4 grazers and fine scratches more typical of C_3 grass consumption due to possible phytolith size variation and differential silica content (Hummel et al. 2010). Therefore, microwear could provide another insight into the climate (supporting C_3 or C_4 vegetation dominance accordingly) and consequential dietary adaptations for *Antidorcas*.

The microscopic wear patterning produced by succulents has not been considered in detail but may be a consideration here, as modern springbok are known to consume certain succulent species. The majority of succulents adopt the CAM photosynthetic pathway (see chapter 10 'Isotopes analysis' for definition). CAM plants typically invest heavily in herbivory defence due to the high energy cost of adopting the CAM photosynthetic pathway. With this in mind, the likely DMTA signal obtained may be expected to be similar to a browsing signal. CAM plants are typically restricted to arid conditions, suggesting high levels of dust/grit and related abrasion would also be prevalent associations with these plants.

However, microwear profile images are rarely that simple to interpret and there are many factors to consider prior to conclusively associating dental microwear patterns with any particular diet. For example, grit, or silica particles (phytoliths) found in monocot grasses, often associated with grazing, can cause pitting of the enamel surface (pits), thereby skewing the grazing signal somewhat. Yet these findings do not undermine the usefulness

of microwear analysis. Increased grit in the diet can be indicative of low-level grazing, i.e. feeding close to the ground (Healy and Ludwig 1965). Based on stable carbon isotope analysis, it is believed that *Antidorcas bondi*, for example, was last in a line of grazing succession (Brink and Lee-Thorp; Brink 2016) as detailed in chapter 3 (‘*Antidorcas’*), feeding on the small shoots closest to the ground. Research to date would suggest that diet creates a more prominent microwear impact than exogenous particles (e.g. Merceron et al. 2016 feeding experiments; but see Wood 2013; Lucas et al. 2014). However, *A. bondi* as a believed low-level feeder may incorporate high levels of dust and/or grit into the microwear signal that may be subtly apparent via DMTA. For instance, a higher microscopic pit prevalence, and/ or high abrasion, could be indicative of grit and go some way to confirming this grazing succession hypothesis. In terms of specific DMTA variables, low-level grazing might be expected to show as lower heterogeneity (dust/grit of more uniform size than mixed browse particles).

Microwear as a palaeoenvironmental indicator

Combined dietary signals obtained via DMTA, allow inferences to be made regarding vegetation present and therefore, of palaeoenvironmental conditions. For example, a dominance of grazing signals is inferred as indicative of savannah landscapes; varying diets within one geographic and temporal range is likely indicative of mosaic habitats (e.g. savanna grasslands and woodland forest habitats present within the shared landscape).

Yet beyond simple extrapolation of dietary indicators to inform on likely vegetation cover, other palaeoenvironmental indicators can be detected through microwear analysis. For example, it has been hypothesized that dust covered grasses would result in greater abrasion and potential decreased pit percentage (Shubert et al. 2006) due to the abrasive nature of dust/sand particles and consequent overwriting of wear scarring. This in turn could be reflective of climatic shifts or events, such as the aolian dust fluctuations throughout the Plio-Pleistocene, which increased gradually in concentration and flux from c. 2.8 Ma (deMenocal 2004), as such, abrasive microwear signatures reflected on the *Antidorcas* enamel surfaces may be expected to gradually increase. However, considerable research has focused on the nature of microwear signatures in whether dust and grit do cloud the dietary signals obtained. Ungar et al. (2016) and Merceron et al. (2016) show that overall, microwear data is more informative of dietary preferences and therefore, about palaeovegetation.

Further, the dietary plasticity of *Antidorcas* has the potential to mirror climatic variations. As a mixed-feeder, consuming a greater array of the vegetation present (dictated largely by climatic influences), the dominant dietary strategy would be visible via shifting DMTA signals through time, indicative of associated climatic shifts. For instance, Berlioz et al. (2018) found the mixed-feeding European large deer, *Eucladoceros* to be reflective of glacial (grazing signal), interglacial (browsing signal) events.

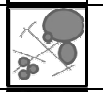
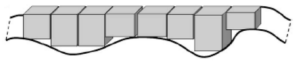
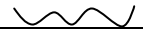
DMTA variables

Complexity (Area-scale fractal complexity, Asfc) measures the roughness of the dental facet surface. Scale of maximum complexity (Smc) shows the scale range Asfc is calculated from (taking the steepest part of the relative area against the scale of the curve).

Anisotropy (epLsar) considers the direction of wear and relative lengths of vectors (depth profiles), essentially providing a view of direction of wear and a glimpse into heterogeneity (Scott et al. 2006). Multiple scratches with no pitting would produce anisotropic surfaces with a high epLsar value, indicating of grazing. Whereas a surface with scratches in opposing directions coupled with pits of varying depths and sizes would produce a complex (high Asfc) and isotropic (low epLsar) surface and be more indicative of browsing diets (Scott et al. 2012, 2006). Homogeneity of wear is provided through HAsfc values (Heterogeneity of Area-scale fractal complexity). Higher HAsfc values indicate greater variation in diet. Homogeneity of diet tends to show in homogeneity of surface texture (i.e. lower HAsfc values) (Scott et al. 2006). HAsfc is calculated through a 9- and an 81-cell mesh over each scanned surface. Tfv (Textural fill volume) values represent the surface texture based on fill volume at different scales (i.e. the relief of the surface) (Scott et al. 2006). Textural 'fill' derives from a cuboid representation of the parameter (see Table 4.5), in which the relative number of cuboids, and their volume, that fit into a cross-section of the enamel surface, is indicative of enamel surface wear depth and uniformity thereof (Scott et al. 2006).

Glossary

Table 4.5: Glossary of DMTA nomenclature used. Parameters are based on established protocols (e.g. Ungar et al 2003, Scott et al. 2005, 2006), Tfv images from Scott et al. (2006).

Acronym	Description	Diet	Typical DMTA image
Asfc	Area scale fractal complexity; surface roughness (complexity)	Grazer; low Asfc	
		Browser; high Asfc	
EpLsar	Length-scale anisotropy of relief; direction and consistency of wear (anisotropy)	Grazer; high epLsar	
		Browser; low epLsar	
HAsfc	Heterogeneity of Area scale fractal complexity Measured scales used for HAsfc for this research: 3 squares x 3 squares (3x3) 9 cell; 9 squares by 9 squares (9x9) 81 cell	Grazer; low HAsfc	
		Leaf browser; Low-medium HAsfc	
		Mixed/ fruit browser; High HAsfc	
Tfv	Textural Fill Volume (shape and texture of the surface) at a fine (a) and coarse (b) scale. A  B 	Higher values (Mixed-feeding)	More cuboids fit; deeper, larger wear 
		Lower values	
Smc	Scale of maximum complexity	Grazer	Fine scale
		Browser	Coarse scale

Acronym	Description	Diet	Typical DMTA image
S.E.M.	Scanning electron microscopy	x	x
SSFA	Scale sensitive fractal analysis	x	x
DMTA	Dental Microwear Texture Analysis	x	x
DASTA	Dental Area Surface Texture Analysis	x	x

4.5.1 CONSIDERATIONS

Phylogeny: The structure and formation of a tooth, especially the enamel and dentine components, vary between species. The properties of the enamel presumably play a part in enamel susceptibility to microscopic damage (the microwear signature). The extent to which enamel properties play a part is not clear for *Antidorcas.* However, Mihlbachler and colleagues (2016) found that, in Perissodactyls, phylogeny and diet influence microwear signals equally. As discussed in the 'measurements' section (4.3), enamel-thickness can give a longer-term indicator of the 'hardness' of the animal's diet (Lucas et al. 2008). If coupled with an examination of the formation and evolution enamel-dentine junction (with relative indication of enamel thickness), a greater insight could hopefully be gained for *Antidorcas* specifically. However, this is beyond the scope of the current research project.

Extensive research has been conducted into the most appropriate facet and combination of facets to sample to obtain a reliable dietary signal (e.g. Merceron et al. 2016; Ramdarshan et al 2016, 2017), reducing as far as possible the phylogenetic impact, to promote a clear palaeodietary signal independent of taxon.

Overwriting: Microwear signals can be confused due to reflecting slightly differing time scales for individuals. The 'Last Supper' effect (Grine 1986) is a process whereby new wear marks replace those underneath (i.e. there is significant and repetitive 'overwriting' making the microwear signature indicative of only the last, or last few, meals of the individual). This occurs more frequently with high levels of dietary abrasion. Thus, it is more likely to be seen in hypsodont bovids, associated with increased wear rates and abrasion of the tooth generally (e.g. Janis 1998). This link provides an insight into how mesowear and microwear analysis can really complement one another to provide a more complete picture.

Typically, browsing diets with lower abrasion, on higher-crowned teeth, require longer timeframes and greater vegetation consumption to overwrite previous scarring (Schulz et al. 2013). Deeper pits take longer to overwrite, as there are more 'layers' to go through before overwriting occurs. In contrast, obligate-grazers have a comparatively high degree of abrasion (Kaiser et al. 2009). High abrasion diets encourage constant 'overwriting', resulting in a uniform anisotropic wear pattern on the enamel surface (Schulz et al. 2013). Mixed feeders, such as *Antidorcas*, often differ from habitual grazers by having more pits remaining on the surface from a browsing phase (Solounias and Semprebon 2002), even if consuming graze relatively soon before death. Mixed feeders may be more difficult to differentiate from obligate browsers but tend to have less extreme complexity with greater heterogeneity and more variability in DMTA parameters, particularly Tfv.

Taphonomy: When considering dentition from archaeological assemblages, microscopic wear features may be either obliterated or created, as an artefact of taphonomic processes (such as the effects of sand particles on deposited dentition). The typically shallow, homogenous, anisotropic scratches characteristic of grazers are believed to not be as easily replicated by naturally occurring taphonomic processes, whereas taphonomic processes can produce similar pit and/or abrasion features to those produced by diet, indicative of browsing (King et al. 1999). A comparison with modern microwear analysis (section 6.1.3) is used to examine the need for an 'off-set' to allow for potential taphonomic influences (Schubert et al. 2006).

Moreover, the nature of cave deposits, with karst water presents the possibility of wetter refugia at certain times within any given landscape, therefore likely to over represent the browse content of the landscape (Stewart pers comm.). This would dampen the palaeoenvironmental signal obtainable somewhat. To negate this issue, consistent site types (i.e. open air, not cave deposit) would need to be compared from East and South Africa to answer similar research questions. This is not currently a possibility due to the reality of hominin-bearing sites in South Africa being predominantly from cave deposits.

4.5.2 Dental Microwear Texture Analysis Method

Specimens were cleaned using acetone-soaked toothbrushes and cotton buds. All specimens were cleaned once with a toothbrush, followed by twice with cotton buds, with 3-5 minutes between each round of cleaning. Negative dental moulds were made using a polyvinylsiloxane elastomer (Regular Body President, Coltene President MicroSystems), a dental grade material which easily peels away from the tooth once dried (drying takes only a few seconds) with no harm inflicted on the specimen when the impression material is removed. This method focuses on the specific dental facets of interest, (Figure 4.20). At least 2 moulds were made of each tooth.

Inevitably, something of the original scar pattern will be lost or hidden (e.g. by bubbles) when creating the moulds. Creating moulds is deemed by some as a destructive technique and many museums will no longer allow this method to be used on their collections. However, this facet-specific method implemented by Ramdarshan et al. (2016) is intended to be non-destructive.

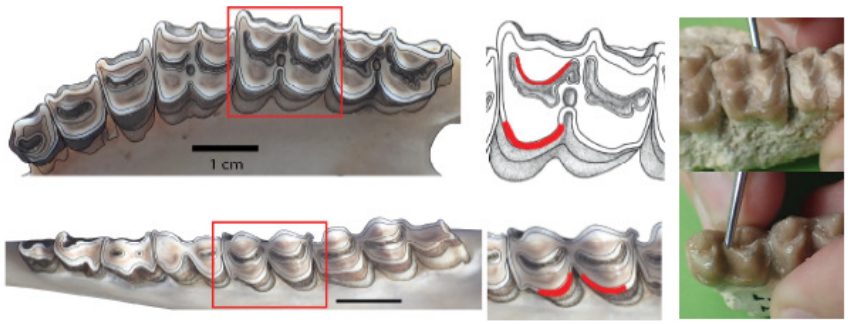


Figure 4.20: Facets used for DMTA sampling. Image from Merceron and Ramdarshan TRIDENT casting protocol 2016 (Ramdarshan et al. 2017). The top image indicates the facets to be scanned on maxillary dentition, primarily the mesio-lingual protocone or paracone; the lower image indicates the facets to be scanned for mandibular dentition, primarily the distal-buccal protoconid.

Moulds were subject to DMTA, analysed at the Laboratoire de Paléontologie, Évolution, Paléoécosystèmes, Paléoprimatologie (PALEVOPRIM; ex-iPHEP), Université de Poitiers in October 2016 and March 2018 under the guidance of Dr Gildas Merceron.

Prepared dental occlusal surface moulds are cut to isolate the facet to be scanned. Ramdarshan et al. (2017) have shown that there are significant differences in dental microwear textures between the disto-buccal facets of the protoconid on lower teeth and the lingual facet of the paracone on upper; but not with the protocone from upper molars (see discussion in Ramdarshan et al. 2017). Primarily, mesio-lingual facets of protocones (upper molars) and distal-buccal facets of protoconids (lower molars) (or on the hypoconid if the former facet is broken) were combined for analyses (see Figure 4.20; Figure 4.21). Research has shown these facets to be comparable (see Ramdarshan et al. 2017).

The mould must be cut as flat as possible to maximise light exposure to the facet surface. The prepared moulds are placed under a Leica DCM8 confocal profilometer using white light confocal technology with a Leica 100x objective (numerical aperture = 0.90; working distance = 0.9 mm). The lateral resolution is an (x, y) interval of 0.129 µm, with a vertical numerical step of 1 nm. Scans are taken in the centre of the facet, where possible, to ensure repeatability and to limit subjectivity. Scans are treated using LeicaMap to eliminate artefacts, such as abnormal peaks following procedures detailed in the supplementary material in Merceron et al. (2016). Artefacts can be due to numerous factors, such as bubbles in the mould or dirt on the facet surface. Some specimens could not be used for microwear due to excessive bubbles, which tends to occur more frequently at higher altitudes (Merceron pers. Comm.); or due to mycellum on the tooth surface masking any microwear damage to the surface. Mycellum growth often favours museum specimens and cannot be removed by acetone alone.

Data analyses for DMTA are run through Sfrax and Toothfrax software, following protocol established by Scott et al. (2005, 2006).

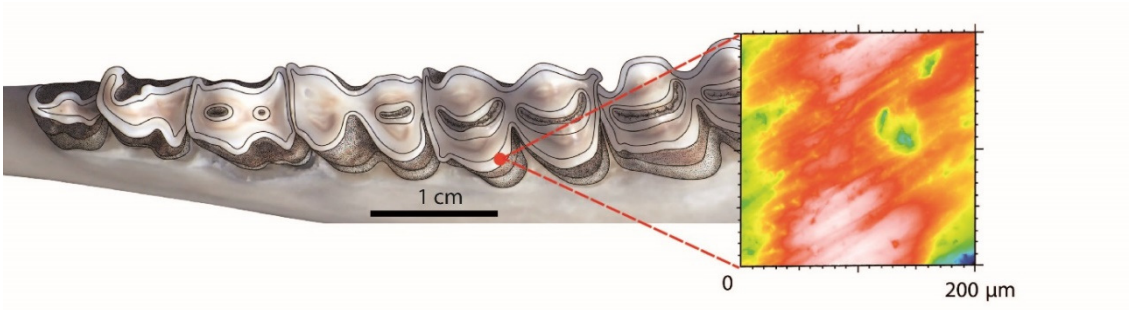


Figure 4.21: Mandibular molar DMTA image: Dental microwear texture analysis is run on the disto-buccal facets of the buccal cuspids along the lower arch (modified from Merceron et al. 2016).

Methodological adjustment

Typically, scans with R^2 values under 0.97µm (minimum angle of the slope) are removed prior to data analysis. However, this would have removed almost 50% of the microwear dataset. Therefore, all scans were re-run on SFrax and ToothFrax after subtracting the polynomial surface in LeicaMap to eliminate the shape of the facet as the principle influencing factor. Francisco et al. (2018) explored the issue of polynomial surface modifications and found no impact was made to DMTA patterns produced. It is suggested

that the unusually concave facet exhibited by certain *Antidorcas* species is indicative of a highly abrasive diet. By comparison, *A. recki* casts tended to not be vulnerable to this issue.

Individual dietary preference can skew the mean signal when grouping at species level (Lehmann et al. 2015). Consequently, individual animal dietary indicators were considered, as well as analysing the mean/median microwear signals for each species for each time period (member).

4.6 Stable Isotope Analysis Method

Examining the carbon and oxygen isotopes within the dental enamel of the various springbok species enables insight into the different dietary components the animals were exposed to as the enamel was being created and mineralised. Used alongside other methodologies, stable isotope analysis provides insight into the diet of now extinct species and allows a re-examination of previous palaeoenvironmental markers.

4.6.1 Carbon Isotopes

Stable carbon isotope ratios of herbivore dental enamel are related to the ^{13}C content of the diet (De Niro and Epstein 1978a, b; Vogel 1978; Tieszen et al. 1983; Kennedy 1988). This is due to the way plants differentially fractionate carbon according to their photosynthetic pathway (Bender 1968; Lee-Thorp et al. 1989; Tieszen 1991), as detailed below.

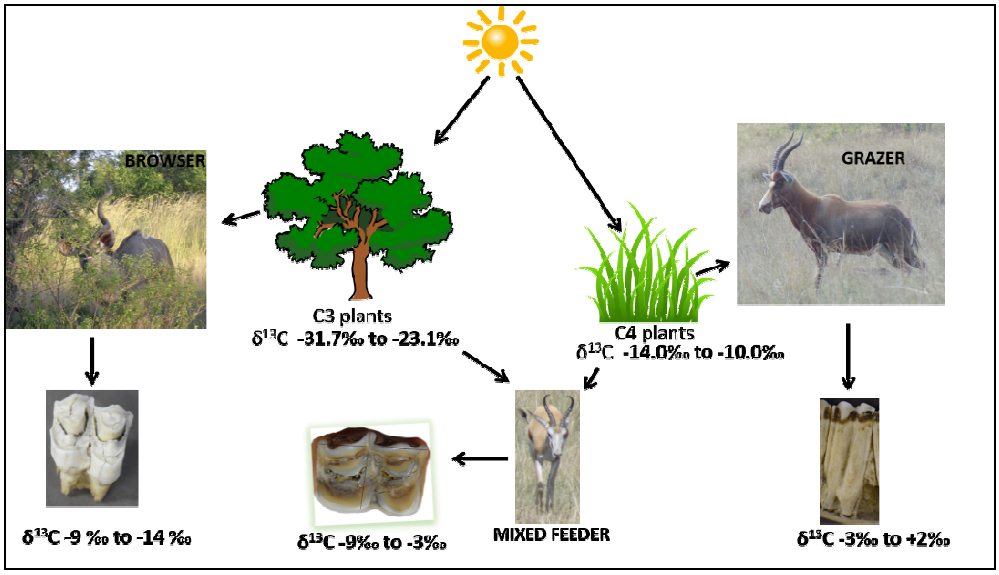


Figure 4.22: Diagrammatical explanation of carbon fixation via photosynthesis. There is a +14.1‰ dietary enrichment from plants to that found in herbivores. The values given by the tooth images are indicative of those expected for each dietary type.

C_3 versus C_4 plants abundance varies depending on climatic condition (C_4 plants preferentially grow under more arid conditions, whereas C_3 plants can inhabit warmer, wetter areas). Care must be taken when inferring climate to ensure seasonality is considered. The percentage of C_3/C_4 consuming animals is suggestive of the relative availability of these plants.

Carbon isotope values of modern South African herbivore values are shown in Figure 4.22 (Sponheimer et al. 2003); >-3.0‰ C_4 dominated, grazing diets; <-9.0‰ C_3 dominated, browsing diet. In between these values, mixed feeding diets are assumed, with values close to the boundaries (i.e. -2.5 to-3.5 and/or -9.5 to -8.5) said to be more variable in their diet.

Dental enamel, a bio-apatite consisting primarily of calcium carbonate, has often been used to reflect the relative proportions of C_3 and C_4 biomass within a particular environment (e.g. Luyt 2001; Lee-Thorp et al. 2007; van der Merwe et al. 2003; Cerling & Harris 1999; Codron 2006; Plummer et al. 2009; Steininger 2011). Isotopic sampling establishes the proportions of C_3 versus C_4 in the diets of herbivores (here, *Antidorcas*). From this, inferences can be made regarding palaeohabitats, i.e. how closed or open the local environment experienced by the herbivore was (Sponheimer and Lee-Thorp 1999b).

Photosynthetic pathways

Plants photosynthesise by absorbing light energy from the sun, absorbed by the plants' chlorophyll. The energy is converted to hydrogen ions and oxygen is given off as a waste product at this point (the light reactions). Using the energy produced by this initial step, carbon is subsequently fixated, taking CO_2 from the atmosphere to convert to sugars. The three photosynthetic pathways differ in how these processes are completed (Forseth 2010).

The different photosynthetic pathways utilised by plant species follow differing methods to fix carbon within the plants' structures. These plants differ in the way they fractionate ^{13}C (Vogel 1978). Thus, the principle factor controlling $\delta^{13}C$ values present in plants (and consequently in herbivore tooth enamel) is the photosynthetic pathway the plant utilises (Smith and Epstein 1971; Tieszen 1991).

Vegetation can reflect climatic conditions, if the relative abundances of C_3 versus C_4 plants (and CAM plants) are evaluated. There are a few factors to consider before inferring climatic conditions, as various factors can impact the vegetation type (according to photosynthetic pathway) that any given environment can support. These factors include soil geochemistry, altitude, climate, disturbance, CO_2 (carbon dioxide) levels, pre-existing canopy cover (and light) and hydrological influences of rainfall and seasonality thereof (Lehmann et al. 2011). The interplay locally of factors (such as soil fertility) with global factors, (such as climate) causes differential habitat-dominance across landscapes. For instance, altitudinal variation has been shown to differentially affect C_3 and C_4 plants proportions (e.g. Stewart and Mitchell 2018).

C_3 pathway

The C_3-Calvin cycle pathway is used by most plants growing in areas with sufficient moisture. For this photosynthetic pathway, the RuBP carboxylase enzyme absorbs CO_2, providing there is sufficient CO2, compared to O_2 (oxygen). If there is too much oxygen, RuBP carboxylase will preferentially absorb the O_2 over the CO_2 (photorespiration), preventing plant growth. If an area is too arid (i.e. sufficient water is not available), excess O_2 builds (is not released through the stomata) and triggers photorespiration. With sufficient moisture (water availability), light reactions and carbon fixation occur simultaneously, allowing almost all of the leaf cells in the plant to produce sugars (Ehleringer and Monson 1993; Forseth 2010).

C_3 vegetation (trees, shrubs, forbs and most temperate grasses) preferably grow in cool growing periods, with higher groundwater levels (Vogel et al. 1978). These plants are

consumed predominantly by browsing herbivores and are considered indicative of a more closed environment (Smith and Epstein 1971; Lee-Thorp et al. 2007; Radloff 2008).

C_4 pathway

The C_4-dicarboxylic acid pathway uses the enzyme PEP carboxylase to absorb CO_2, building carbon in mesophyll cells of the leaf. A 4-carbon chemical compound, oxaloacetate is formed and pumped to bundle sheath cells, where the remainder of the Calvin cycle occurs. Transferring CO_2 between cells within the plant is less energy efficient but more effective to reduce water loss under arid conditions. The PEP carboxylase enzyme is less likely to bind to O_2 than RuBP carboxylase, reducing the chances of photorespiration preferentially occurring under arid conditions. Stomata therefore stay closed for longer, trapping oxygen in the plant (Ehleringer et al. 1997; Forseth 2010). (Hence, higher oxygen $\delta^{18}O$ values are indicative of more arid conditions).

Amongst C_4 vegetation (all angiosperms, most commonly monocotyledons), tropical grasses are prevalent, and the main source of nutrition for grazing herbivores (e.g. Lee-Thorp et al. 2007). C_4 grasses are better competitors in warmer growing seasons with lower but seasonal rainfall (Lehmann et al. 2011). These grasses are primarily consumed by grazers and indicative of an open, grassland environment (Smith and Epstein 1971; Lee-Thorp et al. 2007; Lehmann et al. 2011).

The carbon isotope composition of these plants is greater (heavier) than that of C_3-plants. C_4 plants are more efficient at carbon fixation, allowing them to tolerate drier conditions with lower levels of atmospheric CO_2 but require more energy and are therefore, often outcompeted by C_3 plants under higher carbon dioxide levels (Hopley et al. 2006; Lehmann et al. 2011).

C_4 photosynthesis has a high metabolic cost, relative to C_3 photosynthesis and C_4 plants therefore cannot outcompete C_3 plants to dominate in a low-light environment, such as an area with a pre-existing closed canopy (e.g. dense woodland/forest) (Sage and Kubien 2003) unless there is a disturbance in the C_3 dominated biome (e.g. by fire) (Lehmann et al. 2011).

CAM pathway

This Crassulean Acid Metabolism (CAM) method of fixing carbon is largely confined to shrubs in desert and semi-arid areas of South Africa (Luyt 2001). CO_2 is only absorbed at night, under the coolest conditions, and stored. The stored carbon is converted to sugars (encouraging growth) for a limited period (until carbon stores are depleted) in the daytime. This pathway enables plants to survive incredibly arid conditions but at the expense of rapid plant growth (Bloom and Troughton 1979; Forseth 2010).

The plants utilising this pathway flourish over others in CO_2 or water-deprived areas. This pathway has been relatively ignored as it is thought not to be experienced around the area of the Cradle of Humankind and is rarely used as a food source by savanna herbivores (Codron et al. 2005). It is however, potentially worth considering here as modern springbok (*Antidorcas marsupialis*) will utilise the moisture in succulents (typically CAM plants) when water is scarce.

The CAM pathway alternates between C_3 and C_4 photosynthesis but tends to yield similar C_4 plant-like carbon isotope values (in tropical Africa) in being ^{13}C enriched (Mooney et al. 1977; Codron et al. 2005; Sponheimer et al. 2013; Boom et al. 2014). In southern Africa today, there are 16 families of succulent plants, most of which use the CAM photosynthetic pathway (Mooney et al. 1977).

Palaeovegetation in southern Africa

One of the dominant vegetation biomes visible from fossil evidence is that of savanna landscapes. Savannas are typically open habitats with a substantial C_4 grass layer (Lehmann et al. 2011). In the spread of savannas over the last c. 7 Ma (Cerling et al. 1997), C_4 grasses replaced pre-existing C_3 grasslands (Strömberg 2004) or other C_3 vegetation landscapes, such as forests, thickets and shrublands (Keeley and Rundel 2005). With a combination of disturbance (such as fire) (Lehmann et al. 2011) and low level, seasonal rainfall, C_4 vegetation is a more effective competitor (Orions and Solbrig 1977; Edwards et al. 2010; Lehmann et al. 2011) and capable of dominating the landscapes (spreading savanna grasslands).

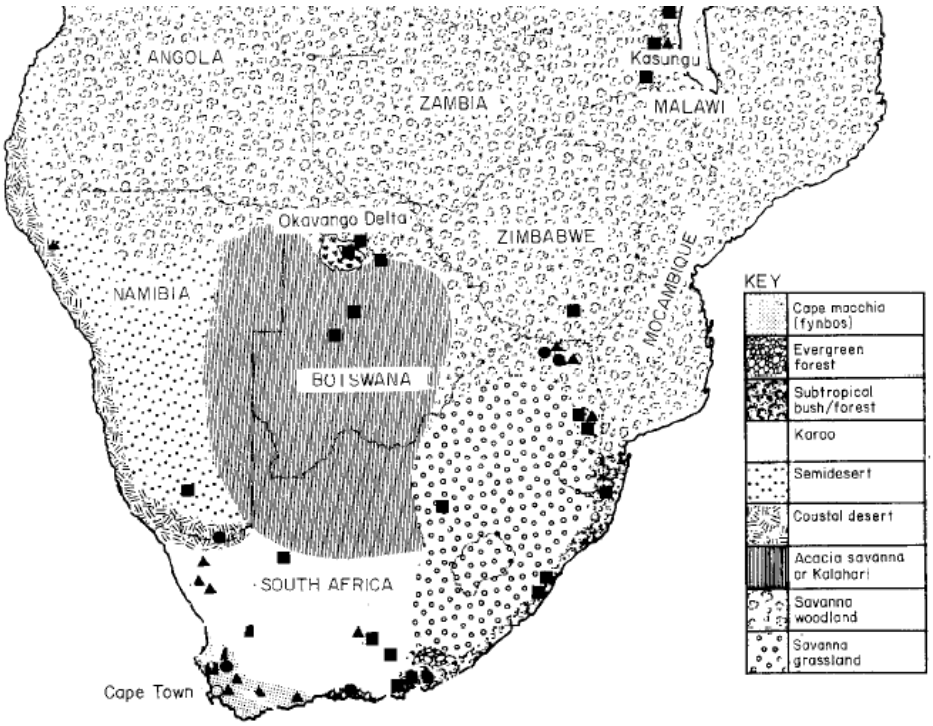


Figure 2. Southern Africa, indicating the principal vegetation zones. Faunal species included: Herbivores (■), *Alcelaphus lichtensteinii, Antidorcas marsupialis, Cephalophus natalensis, Connochaetes gnou, C. taurinus, Damaliscus dorcas, Diceros bicornis, Equus burchelli, E. zebra, Giraffa camelopardalis, Hippopotamus amphibius, Hippotragus equinus, Hystrix africaeaustralis, Phacochoerus aethiopicus, Raphicerus melanotis, Redunca arundinum, Sylvicapra grimmia, Syncerus caffer, Tragelaphus angasii, T. scriptus, T. strepsiceros;* Omnivores (●), *Papio ursinus, Potamochoerus porcus*; Carnivores (▲) *Canis mesomelas, Crocuta crocuta, Felis caracal, F. lybica, F. serval, Genetta genetta, Hyaena brunnea, Lycaon pictus, Otocyon megalotis, Panthera leo, P. pardus, Proteles cristatus, Vulpes chama.*

Figure 4.23: Map depicting the varying vegetation biomes of modern day southern Africa, figure from Lee-Thorp et al. 1989 (page 589, Figure 2).

Carbon isotopes to infer South African palaeoenvironments

Isotope data have assisted in refining palaeoenvironmental reconstructions, e.g. Makapansgat Limeworks 3 was more closed than previously indicated by Vrba (1975,

1982; see chapter 2) as some species assumed to be grazers or mixed feeders based on their extant counterparts, were actually browsers (Sponheimer et al. 1999). Significantly for paleovegetational reconstructions of Sterkfontein, Luyt (2001) noticed a greater mean $\delta^{13}C$ depletion in Sterkfontein Member 4 than in Member 5, suggesting a warming and drying through time from Member 4 accumulation (~2.5 Ma) to Member 5 accumulation (~1.7 Ma). An increase in carbon isotopes $\delta^{13}C$ values through time in *Antidorcas* would support the proposed long-term drying trend (see chapter 2). Using stable isotopes alongside other methods enables further refinement of our understanding of the palaeoenvironmental context from 2.8-0.8 million years ago in southern Africa.

4.6.2 Oxygen Isotopes

The oxygen isotope composition of vertebrate teeth is extensively used as a geochemical means to decipher the palaeoenvironmental air temperature (e.g. Bernard et al. 2009). As plants undergo evapotranspiration, ^{18}O is unevenly distributed through the plant, with leaf water becoming the most enriched in ^{18}O (Gonfiantini et al. 1965; Dawson et al. 2002). Herbivore $\delta^{18}O$ values are dependent on which plant parts are preferentially consumed. Browsers therefore, tend to have enriched $\delta^{18}O$ values as they feed primarily on plant leaves, whereas grazers rely more on regular consumption of drinking (meteoric) water (Cerling et al. 1997; Sponheimer and Lee-Thorp 1999a; Levin et al. 2006; Ecker et al. 2018). Stable oxygen isotopes can inform more on a landscape's aridity, an aspect scarcely obtainable via other means.

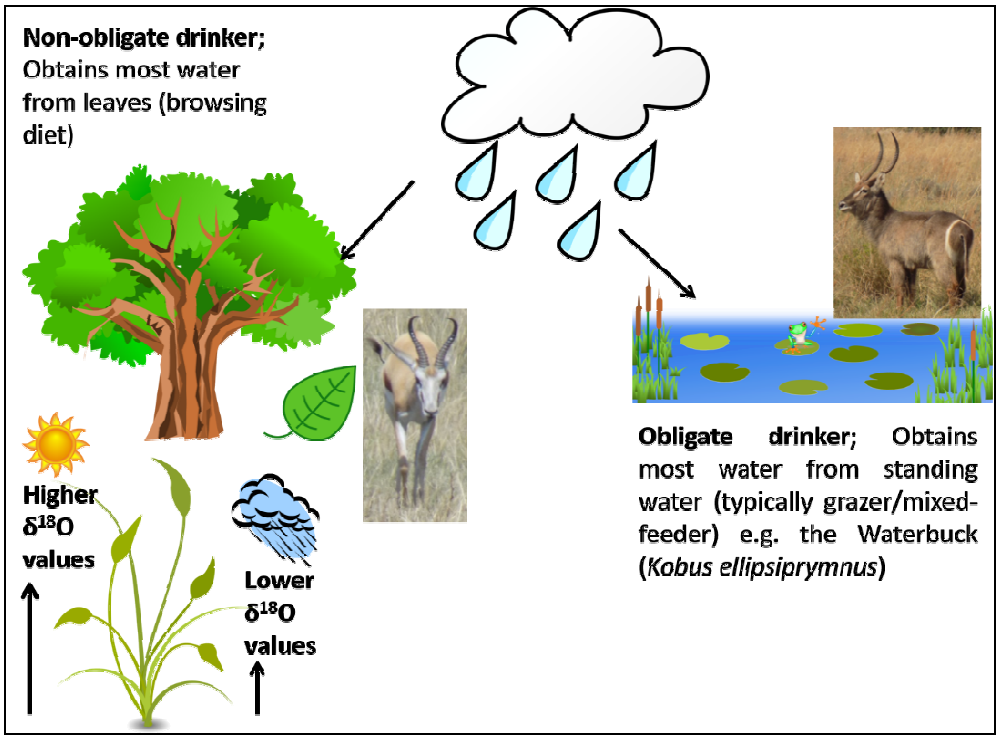


Figure 4.24: Visual explanation of stable oxygen isotope found in bovid dental enamel. On the left, shows non-obligate drinkers, such as A. marsupialis, who obtain the majority of their water via the leaves they consume. This dietary behaviour leaves their oxygen isotope values vulnerable to climatic variability. In more arid conditions, evapotranspiration occurs more rapidly in plants, resulting in the leaves consumed by browsers, being more enriched in $\delta^{18}O$. In contrast, when the temperatures are lower and the environment is wetter, evapotranspiration occurs at a slower rate, therefore, the leaves are depleted in oxygen $\delta^{18}O$, consequently, the ingested and preserved $\delta^{18}O$ in the herbivore is also depleted.

Oxygen isotopes to infer South African palaeoenvironments

Animals' isotopic compositions vary in response to environmental change (Longinelli 1984; Luz et al. 1990; Ayliffee & Chivas 1990). $\delta^{18}O$ values obtained from bovid dental enamel are indicative of water use (predominantly drinking behaviour) and thermoregulatory behaviour (Luyt 2001). Water-dependent animals (i.e. that drink more regularly) have more depleted ^{18}O values than those that obtain their water from plant sources (particularly leaves) (Sponheimer & Lee-Thorp 2001). Water-dependent animals typically have $\delta^{18}O$ values, in line with local precipitation (Bernard et al. 2009; Faith 2018). Knowledge of a taxa's ES-EI (evaporation sensitive or insensitive respectively) has been shown to be of importance when utilising oxygen isotopes from enamel samples to determine aridity levels (Faith 2018). Leaf water is relatively enriched in $H_2{}^{18}O$ due to preferential evapotranspiration of the lighter $H_2{}^{16}O$ molecule (Gonfiantini et al. 1965; Epstein et al. 1977; Sternberg 1989; Yakir 1992). Thus, animals obtaining most of their water via leaf water, as opposed to drinking water, will have enamel more enriched in ^{18}O (Sponheimer & Lee-Thorp 2001). Modern *Antidorcas marsupialis* can survive without drinking water during the dry season and can be considered evaporation-sensitive taxa (obtaining most of their water from leafy dicots). It may be expected that fossil *Antidorcas* was also water-independent, and consequently had $\delta^{18}O$ enrichment.

Oxygen isotopes $^{18}O/^{16}O$ ratios (expressed as $\delta^{18}O$ values) obtained from dental enamel apatite reflect aridity (Levin et al., 2006) along with the oxygen isotope composition of local meteoric water consumed by fossil bovids (Sponheimer and Lee-Thorp, 1999; Podlesak et al., 2008). For non-obligate drinkers, such as *Antidorcas*, typically, higher $\delta^{18}O$ values would imply more arid conditions. Relatively low $\delta^{18}O$ values for non-regular drinking species (obtain the majority of their water intake from plant consumption), such as *Antidorcas marsupialis*, suggests low evapotranspiration rates, and by inference, wetter environmental conditions (Ecker et al. 2018; Sponheimer and Lee-Thorp 1999a).

$\delta^{18}O$ often do not preserve as well as $\delta^{13}C$ values (Wang and Cerling, 1994; Zazzo et al., 2004). Nevertheless, these may be coupled with carbon isotope ratios to reveal the dietary niches of fossil bovids in greater detail (e.g. Luyt et al. 2000; Hare & Sealy 2013). The concentration of oxygen isotopes in meteoric water (which is in turn, taken on by the animals and distributed throughout the tissues (such as dental enamel), and measured through mass spectrometry) is influenced by numerous factors, such as air temperature (Bernard et al. 2009). Levin et al. (2006)'s study on stable isotope aridity index for East African terrestrial mammals highlights how oxygen isotopic composition of mammal tooth enamel ($\delta^{18}O$ values) can be used as an aridity proxy. The study shows the importance of

determining the species' isotopic sensitivity to environmental aridity; evaporation sensitive (these animals $\delta^{18}O$ values increase with aridity) or evaporation insensitive (these animals mirror local meteoric water). $\delta^{18}O$ values from dental enamel of contemporary animals in the same geographic area will record slightly different aspects of the environment; understanding the animal's environmental sensitivity allows their ^{18}O composition of bioapatite to be used to show changes in aridity (Levin et al. 2006).

Blumenthal et al. (2017)'s revised aridity index for quantifying water deficit in terrestrial environments from dental enamel $\delta^{18}O$ has been shown to be a useful tool in assessing palaeoaridity in East Africa. This method is based on the water deficit (i.e. annual difference between water loss (via evaporation/transpiration) and water gain (via precipitation) (Lehmann et al. 2011) and $\delta^{18}O$ enrichment between local meteoric water and that of tooth enamel. As meteoric water cannot be directly known from the fossil record, estimates are made from EI (evaporation insensitive) taxa $\delta^{18}O$ values (Blumenthal et al. 2017; Faith 2018). However, this type of analysis requires many factors to be considered, including, taxonomic identification and understanding of the palaeoecology of the taxa chosen, particularly their water intake (Levin et al. 2006; Kohn et al. 1996; Blumenthal et al. 2017). Although methodologically not directly applicable for this research, this type of analysis has enabled suggestions of decoupling of the long-established link between aridity and increased abundance in C_4 vegetation and grazing; thereby highlighting the importance of other environmental factors that should be considered, such as rainfall and seasonality.

Variation of mean air temperature by only a few degrees, evidenced via often <2‰ $\delta^{18}O$ variations can be indicative of major climatic changes (Zazzo et al. 2004). Inferences of climate or climatic instability may be possible if sufficient variation exists in the oxygen isotope signature, as a result of individual physiological stress and mechanism for thermoregulation. For example, animals that pant to reduce heat loss will have a higher $\delta^{18}O$ value than one that sweats (releasing water and ions through the skin) to allow cooling as isotopically depleted oxygen is being lost in the process of panting (more concentrated water evaporation) (Luyt 2001). This is a useful tool for understanding some of the otherwise intangible behavioural aspects of fossil ecology. For example, observational analysis of modern springbok has shown herd size and associated behaviour is linked to specific rainfall patterns (rather than to seasonal patterns *per se*), which is believed to be due to the lambing season occurring post-rainfall (Stapelberg et al. 2008), when new grasses sprout and nutrition availability is increased. Modern *A. marsupialis* lose significant water via sweating and panting during hot, arid conditions to ensure thermoregulatory needs are met (Hofmeyr and Louw 1987). Modern *A. marsupialis* is able to survive without drinking water provided their food content contains over 10% moisture (Greenwald 1967) but they will drink water when it is in abundance (Bigalke 1972; Nagy and Knight 1994; Skinner and Louw 1996). Behavioural adaptations, such as nocturnal feeding and selective feeding of shrubs with high water content enable this type of non-obligate water activity (Shortridge 1934; Nagy and Knight 1994; Bigalke 1972). Although the same can only be inferred for fossil *Antidorcas* species, here the assumption is made that all *Antidorcas*

species were not obligate drinkers, and the stable oxygen content of their dental enamel is predominantly reflective of aridity levels.

Dental enamel $\delta^{18}O$ variations are reflective of seasonal food and drinking water $\delta^{18}O$. Other factors, such as weaning may play a part in the variations seen but precipitation levels are the dominant contributor in the variation of $\delta^{18}O$ in bovid enamel (Luyt & Sealy 2018). Seasonal precipitation variations are averaged in the enamel values, as seasonal variations would have been experienced by the individual during enamel formation. Seasonal factors influence $\delta^{18}O$ of teeth that are forming and mineralising at the time (Bryant et al. 1996; Murphy et al. 2007b; Tornero et al. 2016), are shown via serial samples from individual teeth.

As some of the oxygen is derived from vegetation consumed and respiration, the enamel oxygen isotope values are not *completely* indicative of precipitation levels. No discernible weaning signal or difference across the toothrow has been found when testing the method (e.g Luyt & Sealy 2018).

Taken together, $\delta^{13}C$ and $\delta^{18}O$ isotope values allow insight into climatic drivers of landscape habitats and consequent niche partitioning (Ecker et al. 2018).

4.6.3 Considerations

Degeneration and preservation The differential taphonomic agents acting upon each assemblage is addressed Appendix A3. Whilst enamel is able to withstand the effects of degeneration and is less susceptible to taphonomic factors compared to bone, some degree of differential degeneration between deposits and between individuals is possible (Luyt 2001). Luyt's (2001) study showed little diagenetic alteration had taken place for the Swartkrans samples. The method implored by Sponheimer (1999) for the pre-treatment of samples limits the possibility of contamination and the impact of taphonomic factors but cannot completely exclude them. Oxygen isotopes are more complex to interpret but are believed to be more prone to diagenetic affects and chemical alteration than carbon isotopes (Wang and Cerling 1994; Luyt 2001).

Contamination Schoeninger et al. (2003) highlighted the possibility of chemical alteration of fossil enamel by the surrounding sediments. The context of archaeological deposit the specimen was found in should be recorded to mitigate this issue if necessary.

Sampling procedure Although experimental evidence often comes from different species, records of intra-tooth variability must be considered to ensure sampling is representative of environmental variability as far as possible. For example, enamel growth of M3 slows exponentially, making consistent sampling distance misrepresentative of consistent time periods (Zazzo et al. 2012). See Table 4.6 for *Antidorcas* dental molar formation, mineralisation and eruption patterns. The mesial side of the tooth records environmental variability more faithfully than the buccal side, and has been proven to show greater intra-tooth variability (Zazzo et al. 2012).

Scale Observed changes may reflect subtle, smaller-scale environmental changes occurring within a longer-term trend (e.g. Hopley 2004; Lee-Thorp et al. 2007). Therefore,

consideration of scale and likely longevity of vegetation change must be taken when making inferences using the isotopic data.

Stable isotopes in dental enamel are fixed during enamel formation, which occurs in the early years of the animal's lifetime, and differs according to tooth type (following dental eruption patterns) (e.g. Balasse 2002). As discussed, microwear analysis is reflective of the last few meals consumed by the animal, using both techniques, alongside the lifetime-averaged mesowear signal, on the same animal's dentition, provides holistic information on diet for the individual animal.

Dental eruption patterns Isotopic sampling provides only a snap-shot signal according to season (if bulk sampled), age of individual and tooth used for analysis. It has been suggested that isotope values vary across the toothrow (Lee-Thorp et al. 1997). Although this has been contested (e.g. D'Ambrosia et al. 2014; Luyt & Sealy 2018), attention is given to tooth choice for sampling. Dental eruption occurs progressively; with enamel being formed as each tooth matures, thus, isotopic ratios will vary accordingly (as the animal ages, until enamel is fully mineralised). Enamel mineralisation is progressive (along the toothrow) but discontinuous (Reade *et al.* 2015).

The season during which this enamel formation occurs and the tooth sampled (and related age of the individual), is likely to yield differential isotopic signals. Diets will differ seasonally and by population, alongside this, nutrient requirements are likely to alter as an individual matures. Serial sampling attempts to capture the seasonal signal, providing the sampling is consistently spaced across the tooth (from cervix to apex) (e.g. Balasse et al. 2002; Zazzo et al. 2002, 2012; Bernard et al. 2009 but see Zazzo et al. 2012). Where bulk sampling is used, the same position on each tooth should be taken where possible to mitigate for the possibility that isotope ratios may vary between different locations on the same tooth (Koch et al. 1989; Balasse 2002).

Table 4.6: Dental eruption ages for Antidorcas, modified after Rautenbach 1971; De Villiers et al. 1985 (Skinner & Louw 1996).

Tooth	**Crown formation and mineralisation**	**Tooth eruption begins**	**Tooth eruption completion**
M1	1-3 months	3-6 months	6 – 10 months
M2	3-7 months	7-15months	9-16 months
M3	7-10 months	10-22months	18–24 months

Typically, modern springbok are capable of breeding at any time of year, and do so opportunistically, following seasonal rains (Skinner and Louw 1996). The rains maximise the landscape's nutritional potential by initiating new grass shoot growth preferred by the springbok. It is possible that the isotope signature for modern springbok is therefore likely to overemphasise high moisture content (depleted $\delta^{18}O$) and grass consumption (more enriched $\delta^{13}C$). Table 4.6 suggests that isotope samples are yielded from *Antidorcas* with a maximum age of 2 years. Therefore, the isotope analysis cannot reflect diet after the springbok was 2 years old (maximum). Springbok lambs are weaned around 4 months (120- days) (Skinner and Louw 1996) and mineralisation occurs early in the animal's life.

Enamel formation (amelogenesis) takes place in two stages, where the enamel matrix is secreted initially and then crystallised to form a densely packed mass of enamel crystallites

(Hillson 2005). Enamel formation occurs prior to dental eruption. For cheek teeth, first molars erupt first, followed by premolars, then second, followed by third molars (Swindler 2002). Mandibular teeth erupt slightly earlier than maxillary teeth (Smith 2000). It was thought that isotopic signatures differed across the toothrow, with the first molar reflecting the weaning signal as it mineralises whilst the lamb is suckling (Passey and Cerling 2002). However, since the lipid content of ungulate milk is low, any effect is likely to be small (Balasse 2002) and recent studies found no weaning signal for either carbon or oxygen isotopes (Luyt & Sealy 2018).

Various studies have investigated the differential toothrow isotopic signals (e.g. Gadbury et al. 2000; Zazzo et al. 2002, 2012; Wang et al. 2008) but found that although there is variation for individuals across the toothrow, there is little evidence of systematic off-sets between the teeth for carbon and no off-set for oxygen isotopes (D'Ambrosia et al. 2014; Luyt & Sealy 2018).

Intra-specific variation and individual preference It is important to consider the dietary niches of animals from the sum of individual feeding preferences (with a population) (Bolnick et al. 2003, 2007) due to the local impact on individualistic food selection (Lehmann et al. 2015). This is especially true of species with a high degree of individual dietary specialization, as has been shown for the modern springbok (Lehmann et al. 2015). That is, although they may be classified as 'mixed feeders' on a species level, individuals may be anywhere along the feeding spectrum (grazing-browsing), rather than having roughly similar proportions of grass and browse. This is especially true of fossil 'populations' which may span many living populations/herds of springbok over hundreds or thousands of years, within one member. This supports earlier discussions for microwear.

4.6.4 Stable Isotope Method

SELECTION

Molars identified to at least genus level as '*Antidorcas*' were isolated for potential sampling. Following the requirements of the respective institutes, those with some degree of breakage were selected preferentially (rather than destroying any prime molars that may be of benefit for taxonomic identification purposes or similar). Where molars fit this selection criteria, an ideal of 4-5 individuals of each *Antidorcas* species per member were selected. This was not always achievable, with some species within members being better represented than others. Those selected were then subject to approval for temporary export and destructive sampling permits from A) The resident institute (the University of the Witwatersrand) and B) SAHRA (South African Heritage Resource Agency).

SAHRA permit reference numbers: 9641 and 2478.

Select sample analysed specifically for this research

Prepared *Antidorcas* enamel samples from Swartkrans were sent to Dr Angela Lamb at the Stable Isotope Facility, British Geological Survey, National Environment Research Council to conduct a pilot study. Carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope data were obtained via VG SIRA 12 mass spectrometer. The results of both isotopes are expressed as per mil (‰) against the VSMOW (Vienna standard mean ocean water) standard, or SMOW and VPDB standards respectively (Hornberger 1995).

Swartkrans Member 1 and 3 isotope values are obtained as a pilot study for a NERC grant and are presented for the first time with this research (see 'Isotopes' chapter 10). Swartkrans Member 2 isotope values from Sewell et al. 2019. All other values are from published sources as detailed in Appendix A8 and chapter 10. Results obtained here (Table 10.3) are compared to previously published results for *Antidorcas* and supplementary species* from relevant time periods and species at these sites (see Table 10.4 and Table 10.5).

* *Damaliscus pygargus* and *Tragelaphus strepsiceros* are used as the C_4 grazing and C_3 browsing ends of the spectrum respectively. Climatic conditions are likely to affect fractionation in plants and therefore the signal left in the dental enamel of the fauna consuming them (Lee-Thorp et al. 1994; Lee-Thorp et al. 2000; Luyt 2001). By including supplementary species, the grazing-browsing spectrum shift according to climatic conditions can be established.

SAMPLING

Once dental enamel powder is sampled (conducted personally at Bournemouth University), isotopic ratios can be measured using mass spectrometry to separate the different isotopes based on their mass-to-charge ratio (Breci 2017).

Each tooth was considered for bulk or serial sampling. Initial sampling was limited to a 'pilot study' of a maximum of 30 samples. Consequently, only the Swartkrans material was prioritised (as Swartkrans Member 2 isotope samples had already been completed by Dr Sally Reynolds and Dr Philip Hopley at the University of Liverpool in 2002; this data was therefore available to be combined to additional results gained here). 4 specimens (SKX 28008- *A. marsupialis*, Swartkrans Member 3; SKX 34249- *Antidorcas* sp., Swartkrans Member 3; SKX 10703- *A. marsupialis*, Swartkrans Member 1 LB and SKX 11602- *A. australis*, Swartkrans Member 1 LB) were identified for serial sampling, based on their provenance and species identification. Of these 4, 3 were serial sampled. SKX 10703 was bulk sampled to minimize damage due to cracks on the tooth (serial sampling is invasive over a larger area of the tooth and was deemed likely to cause more damage than bulk sampling).

The tooth surface was cleaned with acetone to remove any soil/other potential contaminants. The surface was cleaned by abrasion if sediment was attached. A Dremel (model 8200) with 1mm diamond-tipped drill bit was used on a low speed to obtain dental enamel samples from selected *Antidorcas* molars. The Dremel was cleaned with spray duster and acetone between each sample. The samples were collected in a 1.5 ml Ependorf© centrifuge tube. Each tube was weighed before and after the sample was collected.

The tooth was drilled according to the appropriate sampling method indicated below. In each case, the tooth was held on smooth paper to catch the enamel powder. The paper was used as a funnel to ensure all the enamel powder was tipped into the tube. If small pieces of enamel broke off (rather than as ground powder), these pieces were separated and ground into a powder in a pestle and mortar before being added to the sample.

Enamel samples were taken from the same location for each tooth where possible to allow the best chance at comparative results. As discussed above, the location of the sample obtained can reflect a different part of the animal's life, due to the enamel mineralization process (Reade et al. 2015). Photographs of each specimen were taken before and after sampling to record this destructive sampling.

Enamel powder sample size is dependent on enamel thickness, and for serial sampling, the number of samples depends on the spacing (which should be consistent) and the height of the tooth (i.e. the length of enamel available).

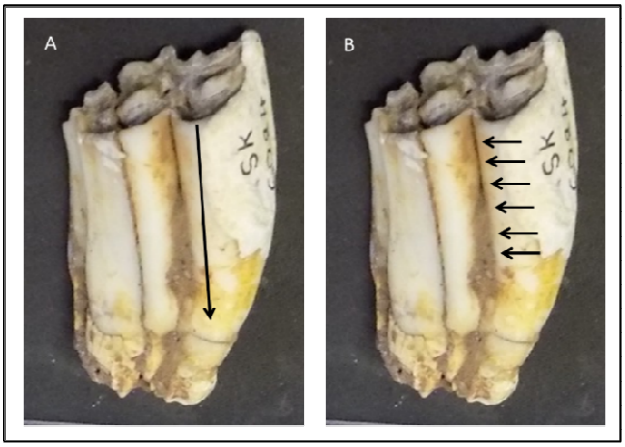


Figure 4.25: Dental enamel sampling: A: Bulk sampling: a single (vertical) sample is obtained. B: Serial sampling: roughly 6 (horizontal) samples are taken, from root to cusp, attempting to reflect seasonal increments.

Serial sampling

Serial sampling attempts to capture the seasonality by taking enamel samples from the tooth root to cusp. It is entirely possible that seasons are missed if the bands of enamel sampled are not consistent, or that a mixture of seasons is obtained if taken along a plane that is not the seasonal delineation. Care is taken to ensure consistency of spacing between enamel samples taken to mitigate for this as far as is achievable.

All equipment and teeth were cleaned after each sample taken. Samples were labelled with their specimen number and a letter to correspond to the sample location (a-f, where 'a' was taken closest to the tooth root/ jawline and 'f' closest to the apex of the tooth). 6 samples for each tooth, with approximately 3-5 mg of enamel powder was desired. In some cases, due to small teeth or thin enamel, this was not possible. This is indicated in the raw data table in Appendix A8.

SPECIMENS SERIAL SAMPLED IN PILOT STUDY: SKX 28008 (Swartkrans Member 3), SKX 34249 (Swartkrans Member 3), SKX 11602 (Swartkrans Member 1).

Bulk sampling

Roughly 7mg of dental enamel powder was obtained (See pre-treatment sheet in appendix A8). Caution to avoid excessive damage to the tooth was exercised. Drilling close to cracks, for example, was avoided where possible.

SPECIMENS BULK SAMPLED IN PILOT STUDY: SKX 34249 (Swartkrans Member 3), SKX 35326 (Swartkrans Member 3), SKX 33839 (Swartkrans Member 3), SKX 10703

(Swartkrans Member 1), SKX 36545 (Swartkrans Member 3), SKX 28999 (Swartkrans Member 3), SKX 10697 (Swartkrans Member 1), SKX 4842 (Swartkrans Member 1).

Pre-treatment

The pre-treatment process was initiated by Lee-Thorp et al. (1997) and considerably refined by Sponheimer (1999), allowing for minimal sample destruction or contamination. Guidance on pre-treatment was given by Dr Philip Hopley at the University of Birkbeck (2017). Samples were pre-treated at Bournemouth University.

1) 2-3mg of powder is obtained from the tooth enamel using a rotary drill with 1.2mm diamond-tipped drill bit.
2) Treat with 1ml of 2% sodium hypochlorite (NaOCL) for 45minutes to remove any organic material.
3) Centrifuge (using 1 standard for each batch of 8 samples).
4) Remove acid with pipette/tip acid out.
5) Rinse 3-4 times with deionised water (18.20hms). Shake tube until cloudy.
6) Place samples in the centrifuge on high speed for 3minutes.
7) Pre-treat with 0.5ml of 0.1M acetic acid for maximum of 15 minutes.
8) Centrifuge (after 10 minutes to ensure acid is removed by 15 minutes).
9) Rinse 3-4 times with deionised water (18.20hms). Shake tube until cloudy.
10) Place the powder sample in the oven overnight at 70°C.

CHAPTER 5

META-ANALYSIS OF FAUNAL COMMUNITIES

5.1 INTRODUCTION

For the majority of this research, *Antidorcas* fossil teeth from selected hominin-bearing sites in southern Africa are used. The sites were chosen as a proxy for the temporal range, rather than a detailed study being conducted on each site chosen. Yet in order to accurately analyse findings obtained via springbok dentition, certain elements of each site's background must be considered. The majority of these issues are discussed in Appendix A3. Here, attention is given to the faunal communities, of which both *Antidorcas* and hominins were a part. The degree of faunal diversity present through time, within a relatively close geographic proximity, can be estimated through a meta-analysis of faunal assemblages recovered from each site. Further, the impact of local factors on faunal distribution and faunal community interactions can be assessed, and considered against the impact of palaeoenvironmental change. This is likely to be visible in sites that are considered roughly contemporary but are geographically distinct. For example, although only just over 1 km apart, the separated sites of Sterkfontein and Swartkrans are believed to temporally overlap in certain Members (Sterkfontein Member 5 and Swartkrans Member 1), any faunal community dynamics differences are likely to be due to local factors. The global and regional climatic influence would also be consistent across both sites (although local scale buffers of such should be considered). Therefore, any discrepancies in faunal community constituents would likely be due to smaller scale influential factors, rather than palaeoclimatic differences.

The faunal communities of sites within the temporal range of 3-0.5 Ma were assessed to place *Antidorcas* data gained from this research into context as far as possible, to understand the characteristics of each assemblage and assemblage formation patterns. This may be impacted by species abundances and taphonomy. Taken alongside site accumulating agents and taphonomic information, as discussed in (Appendices A3) (e.g. Partridge 1986, de Ruiter et al. 2008a,b, Pickering et al. 2004; Behrensmeyer et al. 2000; Adams et al. 2007; Val et al. 2015; Bountalis and Kuhn 2014; Fourvel et al. 2018), a meta-analysis can be used to understand the sites' faunal communities and *Antidorcas'* place within them. Thereby enabling accurate interpretations from the information gained from *Antidorcas* data, as well as placing each site and member in an expected grouping / palaeoenvironment type (from the clusters that group similar sites/Members together).

5.2 CONSIDERATIONS

There are numerous confounding factors that must be considered prior to interpretation of the faunal meta-analysis (Stewart 2008). 1) The difference in taphonomic origin, i.e. how the animals became incorporated into the assemblage; and differential taphonomic processes acting upon the assemblage thereafter; 2) whether the site has been sieved during excavation (and sieve mesh size), which will skew results one way or another for the smaller taxa; 3) taxonomic assignment level, the importance and expertise included for the faunal assemblage during excavation and post-excavation analysis is likely to differ for each site (and potentially for each member if the excavation team alters through the excavation/investigation seasons). Each of these factors may artificially enhance differences between sites, yet, without further research to resolve each of these issues for each site, these potential biases can only be acknowledged.

Taxonomic identification level / Scale

Taxonomic identification levels vary tremendously between site assemblages and are thus likely to create an artefact of difference between sites. To rule this out, identifying only to family or genus level may be required, however, there is then the possibility that this creates false similarities between sites. Thus, taxonomic identification is a major factor, with the level of identification (i.e. to genus/species etc.) and accuracy of identification ultimately plays a part in which assemblages/sites appear most similar.

Some conflicting identifications in the literature also exist for certain sites (e.g. Vrba 1973; Watson 1993; de Ruiter 2001, 2003). Particularly the taxonomic identification of extinct species or genera. For instance, the controversial extinct racoon dog (*Nyctereutes terblanchei*), was assigned to the genus: *Nyctereutes* (e.g. by Turner and Wood 1993), yet if this is the case it would be the only example found in Africa and restricted to the Cradle of Humankind sites. Although researchers provide sound and (metrically argued) arguments against this assignment (e.g Reynolds 2012), the assignment remains in the literature and continues to generate artificial differences between sites on presence/absence analysis, based on taxonomically identified fauna.

Predators

Within any assemblage, their accumulation factors must be taken into consideration. That is, are changes in faunal communities in assemblages a reflection of predator

preference/differing predators rather than changes in environmental conditions and changes in the dietary strategies and habitat preferences of the living faunal communities? When used in conjunction with knowledge of site accumulation, a more holistic overview of the site, its living faunal community and the ultimate taphonomic processes acting upon them as a deposited assemblages and ultimately impacting their representation from the fossil record, is obtained.

Accumulating agents and other confounding factors notwithstanding, it is anticipated that sites accumulating under similar palaeoenvironmental conditions, and therefore having fauna representative of that palaeoenvironment, will cluster together.

Sample size

The overall sample size can impact upon interpretations. If sample sizes are small, this may reflect the taphonomy of the individual site rather than being a reflection of the living biodiversity of the time.

Presence/absence data

Using presence/absence data weighs all species equally within the assemblage, yet only 1 individual of a particular species could be present, giving as much impact on the overall trend as more dominating species, (which could be represented by hundreds of individuals). The relative abundance of different species, particularly bovid species would be of interest for a future study and would add information of the nature and degree of competition and faunal community dynamics. The abundance of bovid species provides an indication of the extent of grasslands within a landscape, where the presence alone of multiple grassland-adapted species cannot give as clear an indication. Many grassland-adapted taxa perhaps hint at more habitat heterogeneity, allowing greater taxonomic diversity in smaller habitat niches across the landscape. Or, suggest far-ranging grassland capable of supporting multiple species that might otherwise compete in a more restricted grassland area. Yet abundance data also has limitations, an example of which is indicated by the reduction in dependence on Vrba's (1980) AAC (Antelopini-Alcelaphini criterion), as detailed elsewhere (see chapter 2).

Presence/absence data is more easily obtainable from the literature. This is partly due to simplicity, with it being easier to identify to genus level or to identify if a species/genus is present but not as easy to determine MNI/ MNE and then which of these is the most reflective and most appropriate for each instance.

5.3 DATA COLLECTION

Faunal lists were assembled for the following sites and deposits:

Table 5.1: Sites (and stratigraphic members) and corresponding site codes used.

SITE CODE	SITE
1	Malapa
2	Gondolin GD1
3	Gondolin GD2
4	Drimolen Main Quarry
5	Sterkfontein Member 4
6	Sterkfontein Member 5 StW 53 Infill
7	Sterkfontein Member 5 East
8	Sterkfontein Member 5 West
9	Sterkfontein Member 5 L/63
10	Sterkfontein unstratified

SITE CODE	SITE
11	Swartkrans Member 1 HR
12	Swartkrans Member 1 LB
13	Swartkrans Member 2
14	Swartkrans Member 3
15	Kromdraai A
16	Kromdraai B
17	Cave of Hearths
18	Wonderwerk Cave
19	Buffalo Cave
20	Gewihaba&Nqumtsa (Botswana)
21	Modern South Africa
22	Modern Botswana
23	Modern Namibia
24	Modern Angola

Additional sites (to those included in the main analyses of this research) were included for this method to place this research into context within southern Africa. A table of presence/absence data of species and genera for each site is analysed. Kromdraai was grouped according to available faunal lists, as A and B but in future studies, as research progresses, Kromdraai should be able to provide more accurate temporal refinement of species presence/absence lists (see Braga et al. 2016). Modern faunal lists were acquired from IUCN Red lists (http://www.iucnredlist.org/ 2018); mammal list for each southern African country inhabited by springbok are used here to provide the degree of intra-genera species variation and presence/absence of genus. Each fossil site (faunal diversity via presence/absence data) can be assessed against modern faunal diversity (presence/absence data) indices to see if they align with any particular modern geographic analogue (areas/ habitat/landscape type) within southern Africa. Although countries are too large to be directly comparable to fossil cave sites (Stewart 2008), this may still enable the degree of biodiversity supported within each fossil site to be estimated.

5.3.1. METHOD

A Hierarchical cluster analysis for binary data was performed in SPSS v.23.software package. This was originally done by nearest neighbour analysis (single linkage) clustering method and squared Euclidean distance measure of proximity and subsequently repeated by average linkage between groups, clustering with squared Euclidean distance proximity measure. There are a numerous methods of clustering that can be used to yield similarities/dissimilarities. A few different methods were considered and included here to highlight where discrepancies may occur based on the clustering method used yet show the consistencies in the results for the faunal communities. In these instances, each method is acknowledged in the relevant dendrogram (a visual representation of clustering) figure caption.

Cluster analyses were conducted for all fossil assemblages at each site within each deposit (references are cited with Table 5.4). Some fossil assemblages (or certain elements/taxa within them) can only be identified to genus level, so by scaling back to genus level, the relationship between sites is perhaps more accurately established than using species-level comparisons. Particularly with fossil taxa, species-level identifications can often require

considerable experience to enable precise identifications; consequently, identifications likely differ between researchers.

The fossil sites were then compared to modern analogues within southern Africa according to presence/absence of genera. This was done at genus level due to the discrepancy between extinct (fossil sites) and extant taxa (modern analogues) at species level. Whilst many of the same lineages exist today, with their ancestral forms present in the fossil sites; if taken at species level, they may not be identified as such due to differing species names. Whilst not taken further here, the range of species present for each site (and deposit) could be inputted to establish potential clustering based on the level of taxonomic variation.

Sites which group first are considered more similar in their faunal assemblages (closer to the Y axis). Single linkage (or nearest neighbour clustering) is one of several methods of hierarchical cluster analysis (Figure 5.2). At each step, the site that is the most similar (the closest site in terms of taxa similarity 'nearest neighbour') is added the cluster, in a step-wise fashion, until all sites are included on the cluster. Equal distances (similarities of taxa) are not assumed (Gower and Ross 1969).

Average linkage (UPGMA) is another method of stepwise agglomerative hierarchical clustering (Sokal and Michener 1958) but uses the mean of all distances (distance between site similarity), compared to the distance between any two sites, to create groupings; assuming a rate of constant distance (distance meaning similarity of taxa present) for each clustering group.

5.4 RESULTS

META-ANALYSIS FAUNAL LISTS

Table 5.2: Genera presence / absence data used for each site (site numerical code as listed in <<table 5.1>>>). Black square / '1' shows the genus was present, '0' in a square, depicts genus absence from the fossil record for this site Member. Data from Berger and Brink 2007; Berger et al. 2015b; Adams et al. 2007, 2016; Adams 2012; Watson 1993, 2004; Keyser et al. 2000; Avery 2001; De Ruiter 2001, 2003; De Ruiter et al. 2008; Kibii 2004; McKee et al. 1995; Reynolds 2005; Reynolds & Kibii 2011; Pickering 1999; Vrba 1974; Brink et al. 2015; Matmon et al. 2012; Kuykendall et al. 1995; Pickford 1990; Val et al. 2015; IUCN 2017).

TAXA	**ORDER**	**SITES**																							
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Dinofelis	Carnivora	1	0	0	1	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Panthera	Carnivora	1	0	1	1	1	1	1	1	0	0	1	1	1	1	1	1	0	0	1	0	1	1	1	1
Genetta	Carnivora	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1
Megantereon	Carnivora	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Machairodontinae indet.	Carnivora	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mungos sp.	Carnivora	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Felis	Carnivora	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	1	1
Felidae indet.	Carnivora	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Proteles sp.	Carnivora	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1
Caracal	Carnivora	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1
Homotherium	Carnivora	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Megantereon	Carnivora	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0
Acinonyx	Carnivora	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	1	1	1
Carnivora indet.	Carnivora	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Atilax	Carnivora	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1
Cynictis	Carnivora	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1
Suricata	Carnivora	0	0	1	0	0	1	1	1	1	0	1	0	1	1	0	0	0	0	0	0	1	1	1	1
cf. Herpestidae	Carnivora	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Herpestes sp.	Carnivora	0	0	0	0	0	1	1	0	1	0	1	1	1	0	0	0	1	0	0	0	1	1	0	1

Vulpes sp.	Carnivora	1	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	1	1	1
Otocyon	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1
Lycaon sp.	Carnivora	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Nyctereutes	Carnivora	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Canis sp.	Carnivora	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	1	0	0	1	1	1	1
Aonyx capensis	Carnivora	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1
Mellivora	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1
Chasmaporthetes sp.	Carnivora	0	0	1	0	1	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Pachycrocuta	Carnivora	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Lycyaenops	Carnivora	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyaena	Carnivora	1	0	0	1	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1
Hyaenidae indet.	Carnivora	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Crocuta	Carnivora	0	0	0	1	1	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1
Leptailurus	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Profelis	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Civettictis	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Nandinia	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Crossarchus	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Galerella	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Helogale	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Ichneumia	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Paracynicitis	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Rhychogale	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Ictonyx	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Peoecilogale	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Lutra	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Atelerix	Carnivora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Manis	Pholidota	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1
Equus	Perissodactyla	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1
Hipparion	Perissodactyla	0	0	0	1	1	0	0	0	0	0	1	1	1	1	1	0	0	1	1	0	0	0	0	0

Diceros	Perissodactyla	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Ceratotherium	Perissodactyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Indeterminate bovid (Size II/III)	Artiodactyla	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indeterminate bovid (Size III)	Artiodactyla	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Large-sized alcelaphine	Artiodactyla	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alcelaphini indet. (medium)	Artiodactyla	0		0	0		0					0		0	0	0	0	0	0	0	0	0	0	0
Alcelaphini indet.	Artiodactyla	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	1	1	1	0	0	0
Bovidae indet.	Artiodactyla	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Megalotragus sp.	Artiodactyla	1	0	1	1	1	0	1	1	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0
Antidorcas	Artiodactyla	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1
Oreotragus	Artiodactyla	1	1	1	1	1	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1
Tragelaphus sp.	Artiodactyla	1	1	1	1	1	0	0	1	0	1	1	0	1	1	1	0	1	0	1	0	1	1	1
Connochaetes sp.	Artiodactyla	0	0	1	1	1	0	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1	1
Damaliscus sp.	Artiodactyla	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1
Raphicerus sp.	Artiodactyla	0	0	1	0	0	0	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1
Redunca sp.	Artiodactyla	0	1	1	1	1	0	0	0	1	0	1	1	1	1	1	0	1	0	1	0	1	1	1
Sylvicapra	Artiodactyla	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kobus	Artiodactyla	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Ourebia	Artiodactyla	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
Taurotragus sp.	Artiodactyla	0	0	0	1	0	0	1	0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0
Gazella sp.	Artiodactyla	0	0	0	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
Boselaphini sp.	Artiodactyla	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kobus	Artiodactyla	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Pelea sp.	Artiodactyla	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	0	0	1	0	0	1	1	0	1
Alcelaphus	Artiodactyla	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1
Hippotragus	Artiodactyla	0	0	0	1	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0

Makapania sp.	Artiodactyla	0	0	0	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Syncerus sp.	Artiodactyla	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	1	1	1	1
Pelorovis sp.	Artiodactyla	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0
Potamochoerus	Artiodactyla	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Kolpochoerus	Artiodactyla	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antilopini sp.	Artiodactyla	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Aepyceros sp.	Artiodactyla	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Hippotragus sp.	Artiodactyla	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1
cf. Pronotochoerus sp.	Artiodactyla	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phacochoerus	Artiodactyla	0	0	0	1	0	0	1	1	0	0	1	1	1	1	1	1	1	0	1	0	1	1	1	1
Tapinochoerus	Artiodactyla	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
cf. Parmularius sp.	Artiodactyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Bos makapania	Artiodactyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Metridiochoerus sp.	Artiodactyla	0	0	1	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Suidae indet.	Artiodactyla	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Giraffidae indet.	Artiodactyla	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
Sivatherium	Artiodactyla	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Hippopotamus sp.	Artiodactyla	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1
Hyemoschus	Artiodactyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Neotragus	Artiodactyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Madoqua	Artiodactyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Cephalophus	Artiodactyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Oryx	Artiodactyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Loxodonta	Proboscidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Papio sp.	Primates	1	0	0	1	1	0	0	0	1	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1
Australopithecus sp.	Primates	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paranthropus	Primates	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0
Homo sp.	Primates	0	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	1	0	0	0	1	1	1	1
Hominidae indet.	Primates	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Theropithecus	Primates	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Parapapio sp.	Primates	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0
Cercopithecidae indet.	Primates	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0
Cercopithecus	Primates	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	1	0	0	1
Leophocebus	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Colobus	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Gorilla	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pan	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Galago	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Galagoides	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Otolemur	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Euoticus	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Allenopithecus	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Miopithecus	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Chlorocebus	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Sciurocheirus	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Perodicticus	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Arctocebus	Primates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Struthio camelus	Struthioniformes	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepus sp.	Lagomorpha	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1
Lagomorpha indet.	Lagomorpha	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Pronolagus sp.	Lagomorpha	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1
Leporidae indet.	Lagomorpha	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Procavia	Hyracoidea	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	0	0	1	1	1	1
Elephas sp.	Proboscidea	0	0	0	1	1	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Elephantidae indet.	Proboscidea	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Myosorex	Eulipotyphla	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0
Suncus	Eulipotyphla	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Chrysospalax	Afrosoricida	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Chlorotalpa	Afrosoricida	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Neamblysomus	Afrosoricida	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Rhinolophus	Chiroptera	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myotis	Chiroptera	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neoromicia	Chiroptera	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orycteropus	Tubulidentata	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1
Bunolagus	Lagomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Poelagus	Lagomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Heterohyrax	Hyracoidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Dendrohyrax	Hyracoidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Macroscelides	Macroscelidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Petrodromus	Macroscelidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Bathyergus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Fukomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Petromus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Thryonomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Anomalurus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anomalurops	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Xerus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Funisciurus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Heliosciurus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Paraxerus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Protexerus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tachyoryctes	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Petromyscus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Cricetomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Saccostomus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Mystomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Lophuromys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Parotomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0

Desmodillus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Gerbillurus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Tatera	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Colomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Grammomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Hybomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hylomyscus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lemniscomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Malacomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Myomyscus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Mylomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Oenomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pelomys	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Chrysochloris	Afrosoricida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Amblysomus	Afrosoricida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Calcochloris	Afrosoricida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Ateleric	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Crocidura	Eulipotyphla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Sylvisorex	Eulipotyphla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Potomogale	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hystrix	Rodentia	0	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	0	1	0	1	1	1	1	0
Mystromys	Rodentia	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Gerbilliscus	Rodentia	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Gerbillus sp.	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Dasymys	Rodentia	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Rhabdomys	Rodentia	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Zelotomys	Rodentia	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Otomys	Rodentia	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Proodontomys	Rodentia	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Rodentia	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

Millardia	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Mus	Rodentia	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Steatomys sp.	Rodentia	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Malacothrix sp.	Rodentia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Dendromus sp.	Rodentia	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Taterillus	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Graphiurus sp.	Rodentia	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Georhychus sp.	Rodentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pedetes sp.	Rodentia	0	0	0	0	0	0	1	0	1	0	1	1	1	1	0	0	0	1	0	1	1	0	1	1
Acomys	Rodentia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Aethomys	Rodentia	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Mastomys	Rodentia	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Thallomys	Rodentia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Cryptomys	Rodentia	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Georychus	Rodentia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Elephantulus sp.	Macroscelidea	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1
Chelonia indet.	Testudines	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Chiroptera indet.	Chiroptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ophidia indet.	Squamata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Eremitalpa	Afrosoricida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0

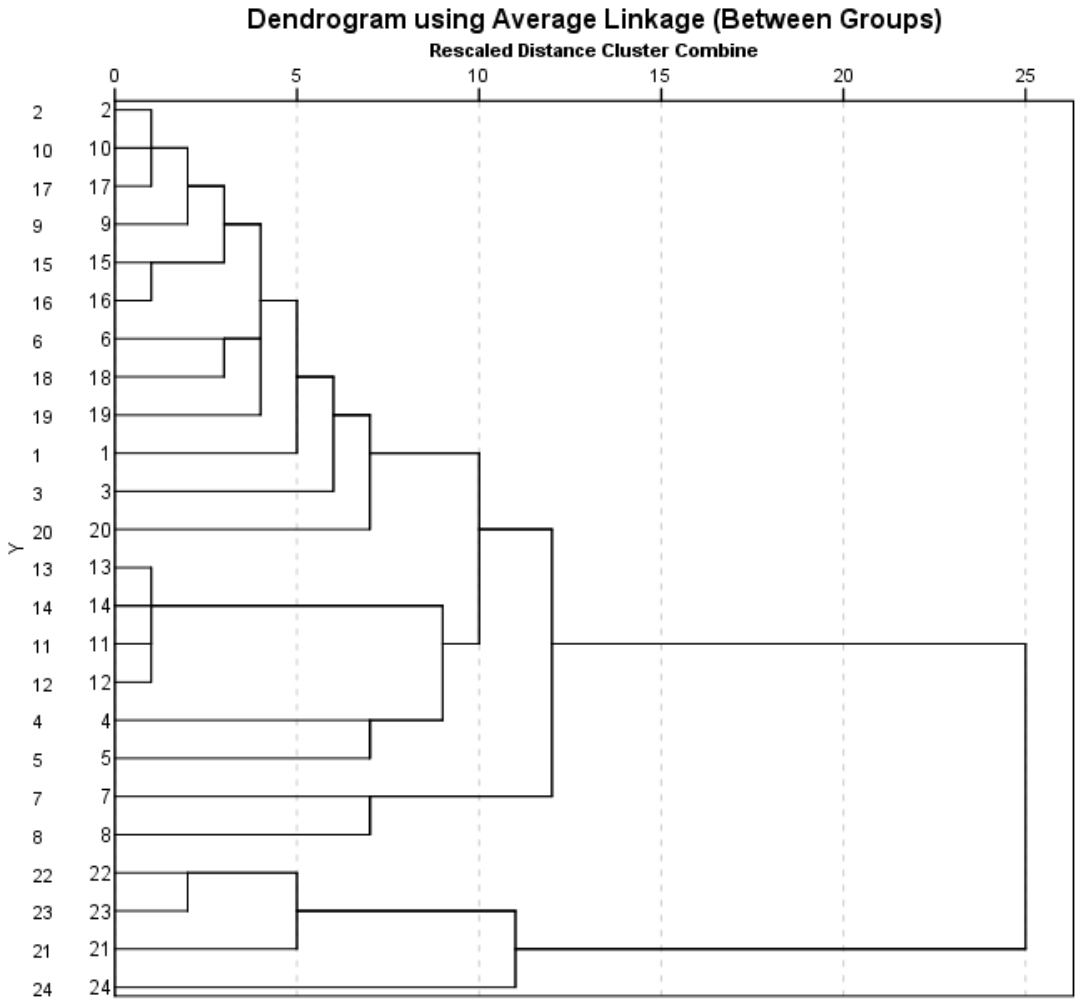


Figure 5.1: Hierarchical cluster analysis dendrogram, with between groups linkage with binary squared Euclidean distance of southern African fossil and modern sites, according to genus present/absent. The Y axis represents the faunal assemblages used, which correspond to the sites as listed in Table 5.1.

Figure 5.1 dendrogram shows the sites that are most similar (branching closest to the Y axis) and those that are least similar (branching furthest from the Y axis). Modern and fossil sites are the least similar, i.e. fossil sites are more similar to other fossil sites than to any modern analogue (sites 21-24 branches at the furthest distance from sites 1-20). The Swartkrans sites are most similar to each other (sites 11-14).

However, that Swartkrans Members cluster together has the potential to be an artefact of faunal records, reported by the same researchers. Taxonomic identification level (i.e. whether identified to genus/species/sub-species level) and method of recovery (sieving/research focus: e.g. zooarchaeology/hominins/lithics) may vary between research groups, when the research group is consistent across the members within a site (as at Swartkrans) but not between sites, the potential for exaggerated differences in faunal assemblages exists.

Of the modern sites, South Africa, Namibia and Botswana are more similar to each other than any are to Angola. Of the fossil sites, Sterkfontein Member 5 East (Oldowan) and West (Acheulean) (sites 7 and 8) are the most dissimilar to any other fossil site.

Sterkfontein Member 4 (site 5) distinction appears stronger using the nearest neighbour cluster method (Figure 5.2) where equal taxa differences between sites are not assumed,

and is shown to be less similar to Drimolen Main Quarry (site 4) than indicated by average linkage (Figure 5.1) which assumes a constant rate of taxa similarity between sites. This means in comparison to all the other sites, Sterkfontein Member 4 and Drimolen Main Quarry are similar but when compared only to one another, they differ.

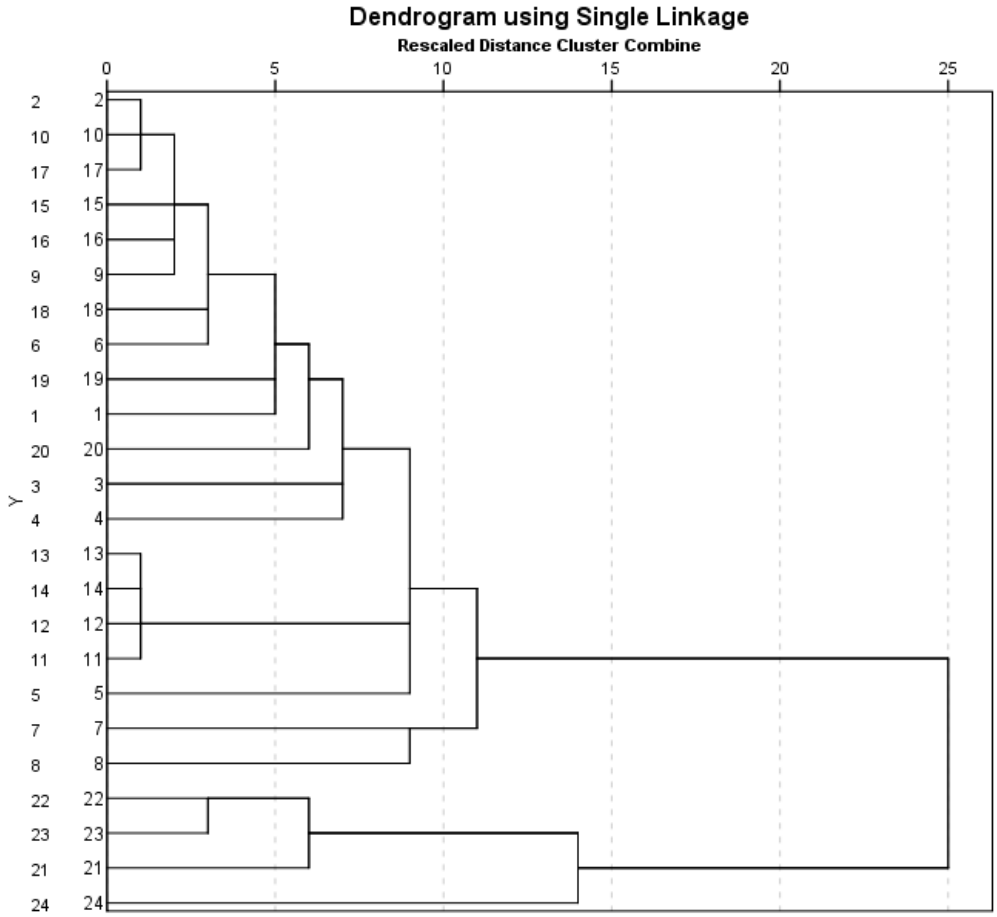


Figure 5.2: Hierarchical cluster analysis dendrogram, with nearest neighbour linkage with binary squared Euclidean distance of southern African fossil and modern sites, according to genus present/absent. The Y axis represents the faunal assemblages used, which correspond to the sites as listed in Table 5.1.

The sites most dissimilar are linked last (separated first, i.e. branch furthest away from the Y axis) in Figure 5.2. The first cluster separates modern from fossil, as may be expected, as modern sites have more of the same (extant) genera across the whole of southern Africa, compared to fossil sites with more extinct genera not present in modern southern African sites, as expected from Stewart (2008). This shows the total level of diversity in the past (combined for the temporal range shown here, 3.0-0.5 Ma) was greater than the range of diversity across southern Africa today.

5.4.1 Micromammals removed

A discriminant function was attempted to see with which modern faunal community each fossil site most closely resembled. Although the discriminant function analysis yielded 91.7 % accuracy, only 2 genera were taken forward in the analysis as accurate predictor variables. The discriminant function analysis was therefore disregarded until more suitable data can be obtained in future research (results presented in Appendix A3 as not successfully used in this research).

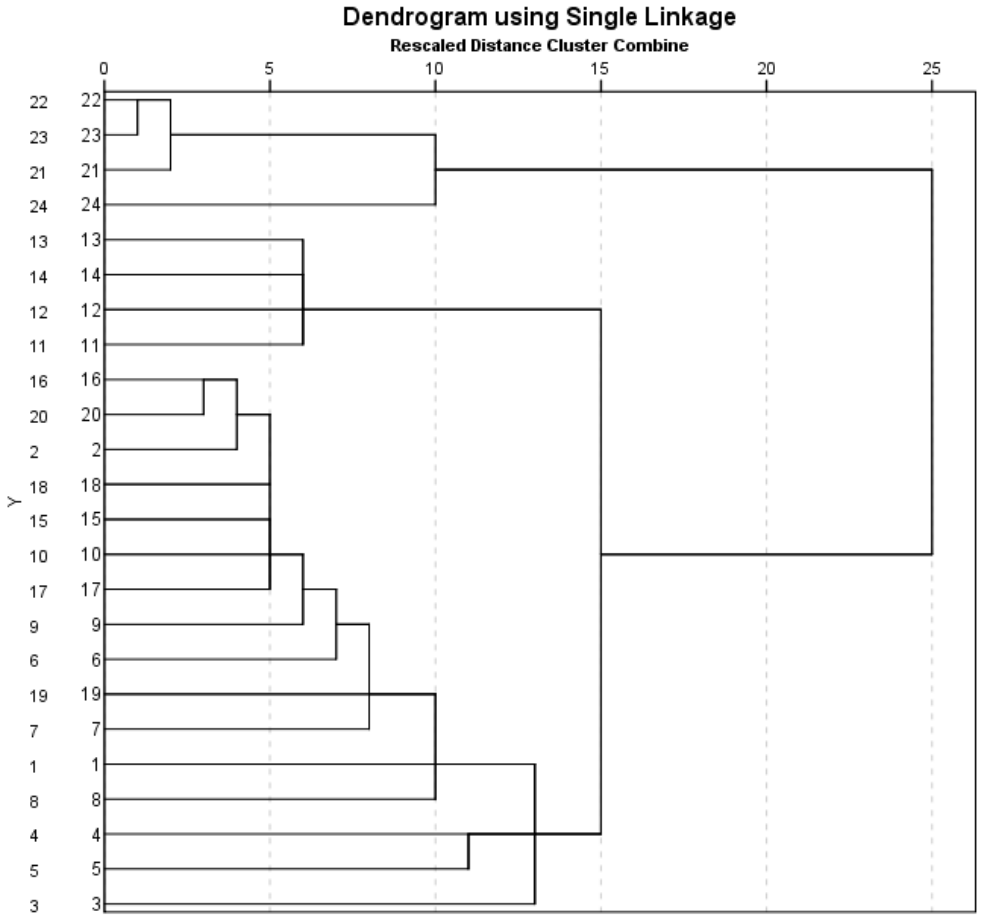


Figure 5.3: Hierachichal cluster analysis dendrogram, using nearest neighbour linkage with binary squared Euclidean distance of southern African fossil and modern sites, according to genus present/absent without micromammal taxa. The Y axis represents the faunal assemblages used, which correspond to the sites as listed in Table 5.1.

Even without micromammals, modern faunal communities are not similar to any fossil faunal community (Figure 5.3). Angola is the more distinct of the modern communities than any of the others are from each other. The Swartkrans Members still group together, suggesting their clustering was not an artefact created by differential sieving at Swartkrans compared to other fossil sites. Of the other fossil sites, Gondolin GD2, Drimolen Main Quarry and Sterkfontein Member 4 appear the most different to the rest of the fossil sites.

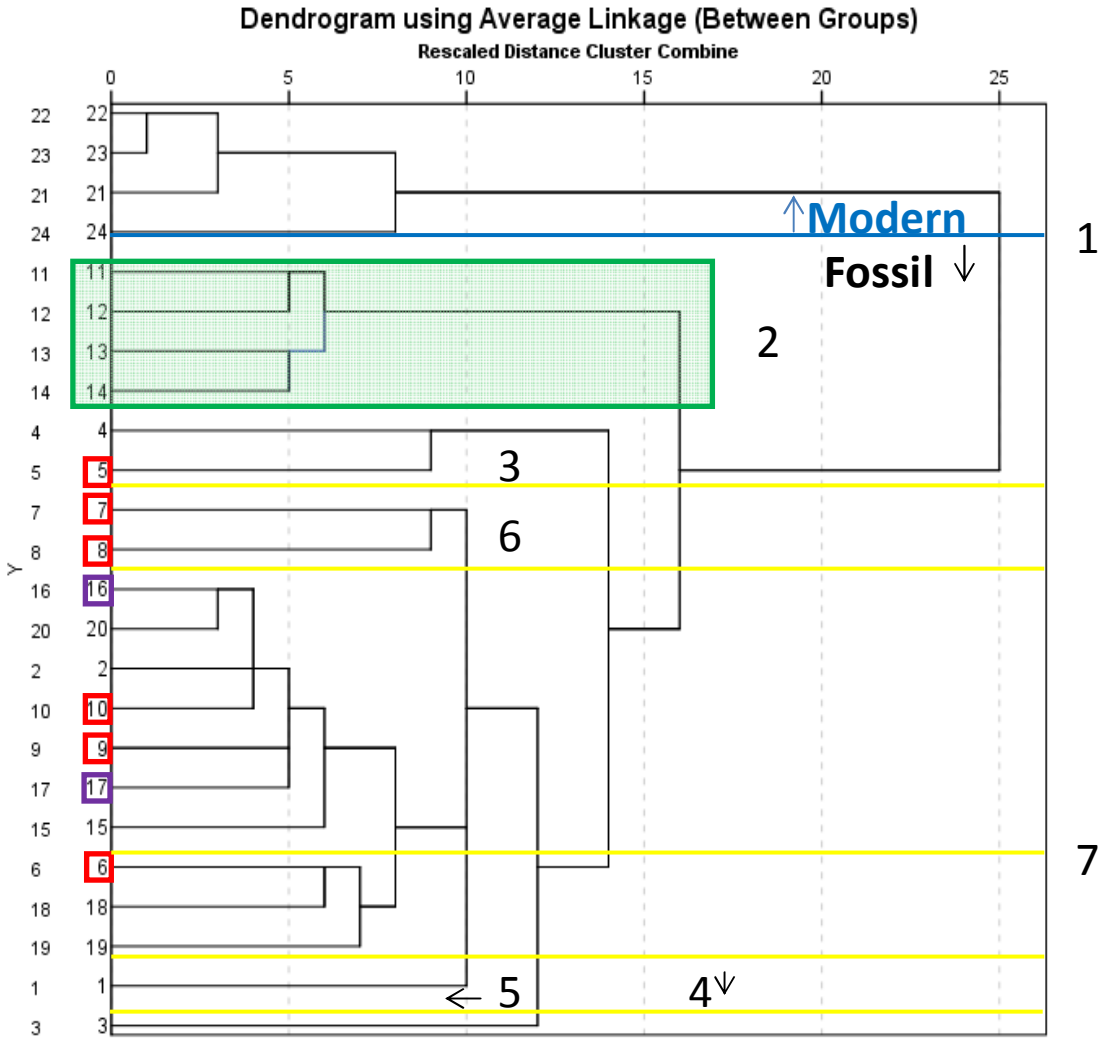


Figure 5.4: Hierarchical cluster analysis dendrogram, between-groups linkage with binary squared Euclidean distance of southern African fossil and modern sites, according to genus present/absent without micromammal taxa. The Y axis represents the faunal assemblages used, which correspond to the sites as listed in Table 5.1. The green box, highlights the first fossil cluster separated, which is all of the Swartkrans Members. The yellow lines delineate clusters, which are numbered according to the stage of separation. Sterkfontein sites are identified by a red square and Kromdraai by purple square.

Again, modern fauna separates first, with no fossil sites being linked to them. Of the modern faunal presence, Angola is the least similar to the others. This would be expected, being closer to the forests of Central Africa with a greater potential for forest taxa to be present. Swartkrans also forms a separate cluster and appear extremely similar in their faunal communities. Drimolen and Sterkfontein M4 are the first of the presumed- to-be-unrelated sites to cluster.

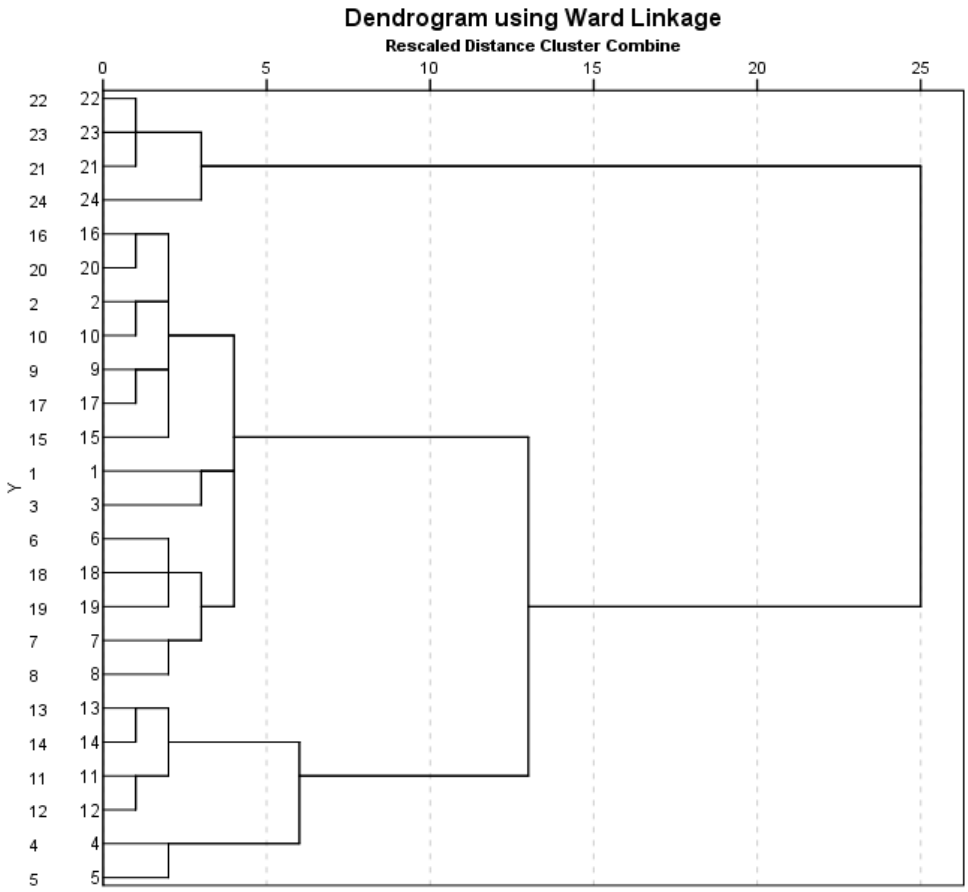


Figure 5.5: Hierarchical cluster analysis dendrogram, by Ward's method with binary squared Euclidean distance of southern African fossil and modern sites, according to genus present/absent without micromammal taxa. The Y axis represents the faunal assemblages used, which correspond to the sites as listed in Table 5.1.

The Ward's method (Figure 5.5) is similar to using nearest neighbour (Figure 5.2) algorithms in assessing minimum variance (Ward 1963). Using the Ward's method, the clusters become more apparent. Again, modern fauna forms a separate cluster from all fossil sites, with Botswana, Namibia and South Africa being more similar than Angola. Sterkfontein Member 4 and Drimolen Main Quarry create a distinct cluster, as do the Swartkrans members; each of which are more similar to each other than any of the other fossil sites. Interestingly, all Swartkrans members next cluster with Drimolen (MQ) and Sterkfontein Member 4. This is perhaps an indication of the range of variation of species within genera that are hidden in this analysis. Based on genera diversity alone, Swartkrans would appear to accommodate more woodland-dominated genera, in line with Sterkfontein Member 4.

5.5 Evaluation: genus level

Distinct clusters form consistently, irrespective of linkage and clustering method. Certain taxa present in their faunal assemblages are therefore scrutinised here to highlight which taxa may be important for creating these clusters and are considered here. Within this, palaeoenvironmental/habitat indicator species may be present and enable insight into potential habitat clustering.

- Swartkrans sites (11-14) compared to 4,5,9,10 (DMQ, Sterkfontein M4, L63 and unstratified) As Swartkrans has been shown to cluster together more than align with any other fossil site, the faunal community dynamics (taxa present and not present) are

considered further. Swartkrans Members continuously group together, suggesting either that their faunal communities were unchanged through time, and/or that the excavation method/ research team focus was unchanged for each member. This is contrasted against the other distinct grouping that formed. As such, the latter is more plausible as Sterkfontein yields roughly contemporary members and sits within the same catchment area for many of the taxa incorporated into each of the assemblages at Sterkfontein and Swartkrans and yet their faunal communities differ.

Table 5.3: Comparative taxa from Swartkrans Members (sites 11-14) and the other distinct group forms (sites 4,5,9 and 10) from certain Sterkfontein Members. 'x' denotes where the taxa IS present, '-' denotes where the taxa has not been published as being present. Micromammals are listed at the end in square brackets but do not act as major contributors to these groupings.

TAXA	**Sites 11-14**	**Sites 4,5,9,10**
Hippopotamus, Sivatherium (extinct giraffid)	x	-
Genetta (genet)	x	-
Acinonyx (cheetah)	x	-
Atilax (marsh mongoose)	x	-
Cynictis (yellow mongoose)	x	-
Otocyon (bat-eared fox)	x	-
Aonyx (African clawless otter)	x	-
Mellivora (Honey Badger)	x	-
Manis (Pangolin)	x	-
Theropithecus (gelada baboon)	x	-
Aepyceros (impala)	-	x
Hippotragus (roan/sable antelope)	-	x
Pronotochoerus	-	x
Pomaochoerus	-	x
Alcelaphus	-	x
Kobus (waterbuck)	-	x
Oerebia (oribi)	-	x
Sylvicapra (duiker)	-	x
Diceros (rhinoceros)	-	x
Lycaon (African wild dog)	-	x
Parahycrocuta (extinct hyaena)	-	x
Lepus (hare)	-	x
[*Orycteropus*]	x	-
[*Myosorex*]	-	x
[*Suncus*]	-	x
[*Mystromys*]	-	x
[*Gerbilliscus*]	-	x
[*Dasymys*]	-	x
[*Rhabdomys*]	-	x
[*Zelatomys*]	-	x
[*Otomys*]	-	x
[*Proodontomys*]	-	x
[*Dendromus*]	-	x
[*Elephantulus*]	-	x

- Sites 4,5,9&10 (DMQ, Sterkfontein M4, L63 and unstratified) clustered together (1st cluster), compared to clustered sites 7&8 (Sterkfontein M5 E and W) (2nd cluster): Again, the level of taxonomic identification creates issue (for example, those not identified to genus level such as 'size II bovid' do not allow direct comparison with other sites that perhaps provided the same taxa as '*Antidorcas*'). The first cluster sites support

more open habitat taxa and have more numerous and different predators (i.e. assemblage accumulating agents).

*Table 5.4: Comparative taxa of distinct groupings from certain Sterkfontein Members (1st cluster: sites 4,5,9 and 10) and (2nd cluster:sites 7-8). 'x' denotes where the taxa IS present, '-' denotes where the taxa has not been published as being present. Micromammals are listed at the end in square brackets but do not act as major contributors to these groupings. *but see Reynolds 2012.*

TAXA	1st cluster	2nd cluster
Megantereon (sabre-toothed cat)	x	-
Vulpes (fox)	x	-
Lycaon (African wild dog)	x	-
Redunca (reedbuck)	x	-
Sylvicapra (duiker)	x	-
Kobus (waterbuck)	x	-
Ourebia (oribi)	x	-
Pelea (rhebok)	x	-
Alcelaphus (hartebeest)	x	-
Syncerus (buffalo)	x	-
Pelorovis (extinct African wild cattle)	x	-
Potamochoerus (red river hog)	x	-
Kolpocherus (extinct pig)	x	-
Hippotragus (roan/sable antelope)	x	-
Pronotochoerus	x	-
Papio (baboon)	x	-
Australopithecus	x	-
Parapapio (extinct baboon)	x	-
Cercopithecus (old world monkey)	x	-
Lepus (hare)	x	-
Mungos (mongoose)	-	x
Nyctereutes (racoon dog)*	-	x
Hipparion (extinct horse)	-	x
Diceros (rhinoceros)	-	x
Paranthropus	-	x
Theropithecus (gelada baboon)	-	x
Struthio (ostrich)	-	x
[*Chrsospalax*]	-	x
[*Chlorotalpa*]	-	x
[*Neamblysomus*]	-	x
[*Rhinolophus*]	-	x
[*Myotis*]	-	x
[*Neoromicia*]	-	x
[*Mus*]	-	x
[*Steatomys*]	-	x
[*Malacothrix*]	-	x
[*Graphiurus*]	-	x
[*Acomys*]	-	x
[*Aethomys*]	-	x
[*Mastomys*]	-	x
[*Thallomys*]	-	x
[*Cryptomys*]	-	x
[*Georychus*]	-	x

5.4.2 Palaeoenvironmental change through time

A Jaquard index was calculated to assess the similarity of sites (Figure 5.6). As the main aim of this research is to consider palaeoenvironmental changes and Sterkfontein Member 4 has been previously shown (e.g. Vrba 1975, Reynolds & Kibii 2011) to be akin to a closed, woodland environment, Sterkfontein Member 4 was chosen as the baseline. Sterkfontein Member 4 is also the earliest dated site used in the rest of this research. Figure 5.6 shows

how similar the faunal communities of each site considered are to Sterkfontein Member 4, and by extension, how similar each faunal community is to a woodland faunal community.

Site 4, Drimolen Main Quarry is the most similar to Sterkfontein Member 4, showing just above 50% similarity. This is followed by Swartkrans (all members) and Sterkfontein Member 5 West, at roughly 40% similarity to Sterkfontein Member 4. The least similar are the fossil sites in Botswana (Gcwihaba and Nqumtsa), followed by Gondolin (GD1), Sterkfontein unstratified, Kromdraai B and Cave of Hearths. All modern analogues appear less than 25% similar to Sterkfontein Member 4 mammalian taxa.

The Gcwihaba Caves in Botswana (roughly 50km from the Sterkfontein Caves), preserve the desert environment (Kalahari) evolution through the Plio-Pleistocene epoch, from c. 2 Ma (https://whc.unesco.org/en/tentativelists/5558/[accessed 30/07/2018].

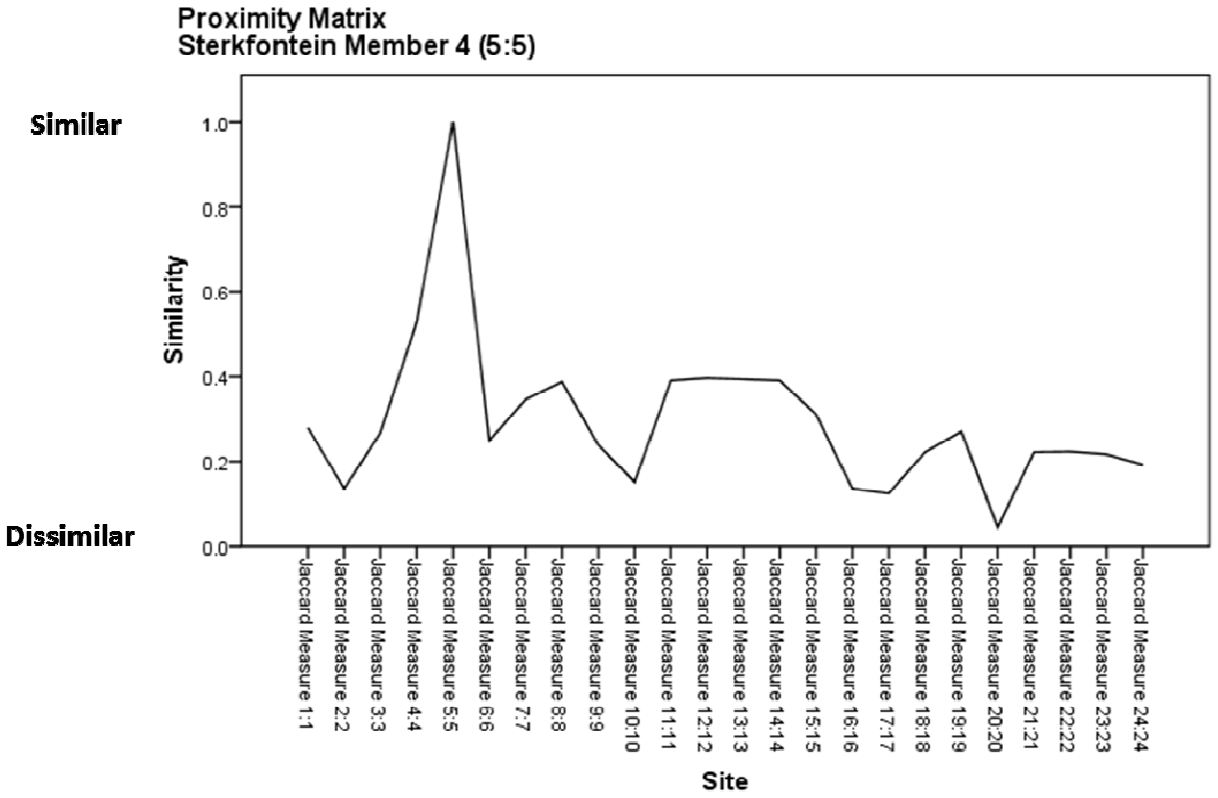
It is not surprising, therefore, that they are support differing taxa to the believed, woodland-dominated palaeohabitats of Sterkfontein Member 4 (c. 2.8-2.0 Ma).

Jaccard Coefficient

To assess the similarity between sites, a Jaccard coefficient of each site to Sterkfontein Member 4 was created (Figure 5.6). The Jaccard coefficient is calculated as follows (Teknomo 2015):

$$Sij = \frac{q + r}{p + q + r}$$

S= the number of taxa absent in both site 1 (Sterkfontein Member 4) and site 2 (each of the other sites, compared in turn); i=Site 1 (Sterkfontein Member 4); j= Site 2 (each other site, compared individually to site 1, in turn); p= number of taxa present in both sites; q= number of taxa present at site 1 but absent at site 2; r= number of taxa absent from site 1 but present at site 2.



Site Code	Site
1	Malapa
2	Gondolin GD1
3	Gondolin GD2
4	Drimolen Main Quarry
5	Sterkfontein Member 4
6	Sterkfontein Member 5 StW 53 Infill
7	Sterkfontein Member 5 East
8	Sterkfontein Member 5 West
9	Sterkfontein Member 5 L/63
10	Sterkfontein unstratified
11	Swartkrans Member 1 HR
12	Swartkrans Member 1 LB
13	Swartkrans Member 2
14	Swartkrans Member 3
15	Kromdraai A
16	Kromdraai B
17	Cave of Hearths
18	Wonderwerk Cave
19	Buffalo Cave
20	Gewihaba&Nqumtsa (Botswana)
21	Modern South Africa
22	Modern Botswana
23	Modern Namibia
24	Modern Angola

Figure 5.6: Jaccard coefficient similarity matrix of faunal communities (genus level) from fossil southern African sites and modern analogues to Sterkfontein Member 4 (category 5:5), (see Table 5.1: Sites (and stratigraphic members) and corresponding site codes used.Table 5.1). Groupings occur for Swartkrans (sites 11-14) and modern (21-24).

Faunal community similarities through time

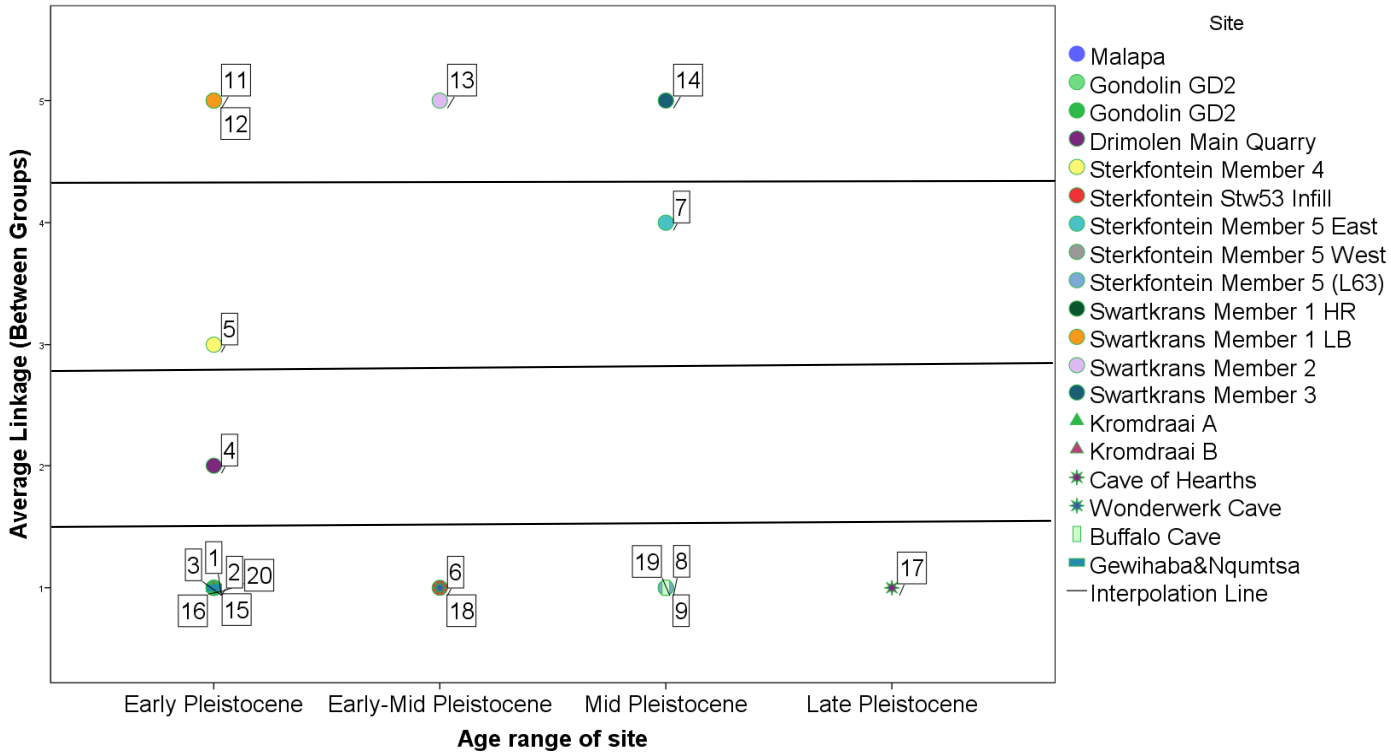


Figure 5.7: Scatterplot showing similarity of taxa present in sites through time (Plio-Pleistocene to late Pleistocene, based on published deposit dates for each site Member), according to average linkage clustering. Numbers shown by the points correspond to number assignments given in Table 5.1. Sites grouped within each horizontal bar are more similar than those within a different horizontal bar. Swartkrans Members show more similarity to each other than to other sites, and are therefore clustered together in the top horizontal bar grouping.

Figure 5.7 shows that the early Pleistocene sites of Sterkfontein Member 4, Drimolen Main Quarry and Swartkrans Member 1 (LB and HR) had dissimilar fauna to each other and to all other early Plesitocene sites (Malapa, Gondolin 1 and 2, Gcwihaba Caves and Kromdraai A and B).

The early-mid Pleistocene Swartkrans Member 2 had a faunal community dissimilar to Sterkfontein Member 5 Stw53 Infill and Wonderwerk Cave.
Sterkfontein Member 5 East (Oldowan) was dissimilar to both Swartkrans Member 3 and to the group of sites including Sterkfontein Member 5 West (Acheulean), Sterkfontein L/63 and Buffalo Cave.

Brief review of clustering methods used

From the methods trialled with the dataset here, both single linkage and average linkage can adequately inform on fossil faunal communities. However, the most appropriate for fossil fauna meta-analysis here is nearest neighbour linkage, as a rate of constant faunal similarity between sites is not assumed.
The Jaquard index, as is often used in ecological studies of living fauna, is useful in comparing multiple other sites/ faunal communities to a specific faunal community/site, as was done here for Sterkfontein Member 4.

5.6 DISCUSSION

The meta-analysis links together similar sites. Whilst there are multiple confounding variables, such as sieving method and cave taphonomy, which must be considered, this analysis is our best tool to distinguish between major site differences, based on faunal assemblages alone.

None of the fossil sites are particularly similar to any modern analogues. Modern South African faunal communities ally the closest with the fossil sites but are more similar to other southern African modern faunal communities than any fossil site.

Sterkfontein appears more disjointed than Swartkrans, with members having diverse faunal communities. Sterkfontein Member 4 has more woodland-dominated fauna than later members (supporting previous reconstructions e.g. Vrba 1973). Sterkfontein Member 4, closely followed by Drimolen Main Quarry, yield the most woodland-associated genera. The most similar assemblages (genus-level) appear in Swartkrans and Sterkfontein Member 5 west. This may indicate a higher woodland-component or perhaps be indicative of the local buffer impact of the Blauubank river (a constant resource and supporting sheltered environments, see chapter 2) for Swartkrans, making Swartkrans able to accommodate these genera locally, regardless of the regional palaeoenvironment.

As Swartkrans faunal communities appear more similar to each other than to any other fossil site, the assumption can be made that any significant differences found throughout this research are less likely to be due to post-depositional taphonomic processes or excavation/researcher bias and more likely to be due to other factors, such as palaeoenvironmental differences. Additionally, all Swartkrans members appear to support more woodland taxa than other South African sites, likely due to the Blaubank river

providing suitable habitats and making the vicinity less vulnerable to environmental changes than more exposed areas (within a water source) (e.g. Cuthbert and Ashley 2014; Cuthbert et al. 2017).

Angola is shown to have the most distinct faunal community of all modern southern African countries in which extant *Antidorcas marsupialis* inhabit. Habitats consistent with the central African rainforest exist within Angola, which is extremely different to habitat types in the rest of southern Africa. This helps support that a meta-analysis at this level works in establishing basic vegetation and habitat differences (via the taxa they support).

This meta-analysis ensures this research is now equipped with knowledge of the faunal community context for the *Antidorcas* assemblages being utilised. With this in mind, the next chapters will assess the palaeovegetation signals, using *Antidorcas* as a bioproxy.

CHAPTER 6

ANTIDORCAS BACKGROUND RESULTS

To ensure accurate interpretations are obtained from the fossil *Antidorcas* dataset, a results summary for modern *Antidorcas* are presented here. Data (dental measurements and use-wear) was collected on modern *Antidorcas marsupialis*, which are incorporated into each methods' results chapter. A summary (from each method) of the modern range of variation is included in this chapter to establish expected intra-specific variability for the genus. The levels of sexual dimorphism and sub-specific variation are explored. This modern *Antidorcas* information can then be used as a base from which to interpret the fossil *Antidorcas*.

This is followed by results of the investigation into the likelihood of the presence of a fourth fossil species, '*Antidorcas australis*' in the fossil contexts at the Cradle of Humankind sites.

SECTION 1: DATA SUMMARY FOR MODERN *A. MARSUPIALIS*

Each subsequent chapter includes data from modern *Antidorcas marsupialis*, from which summaries are presented here (see chapter 4 and chapters 7-11 for an explanation of each method and variables therein). This section provides the range of variation for the extant *A. marsupialis*, to establish the uniformitarian analogue for fossil *Antidorcas*. Additional supplementary information was gained to establish grazer-browser parameters from taxa of known dietary type (as introduced in chapter 3)

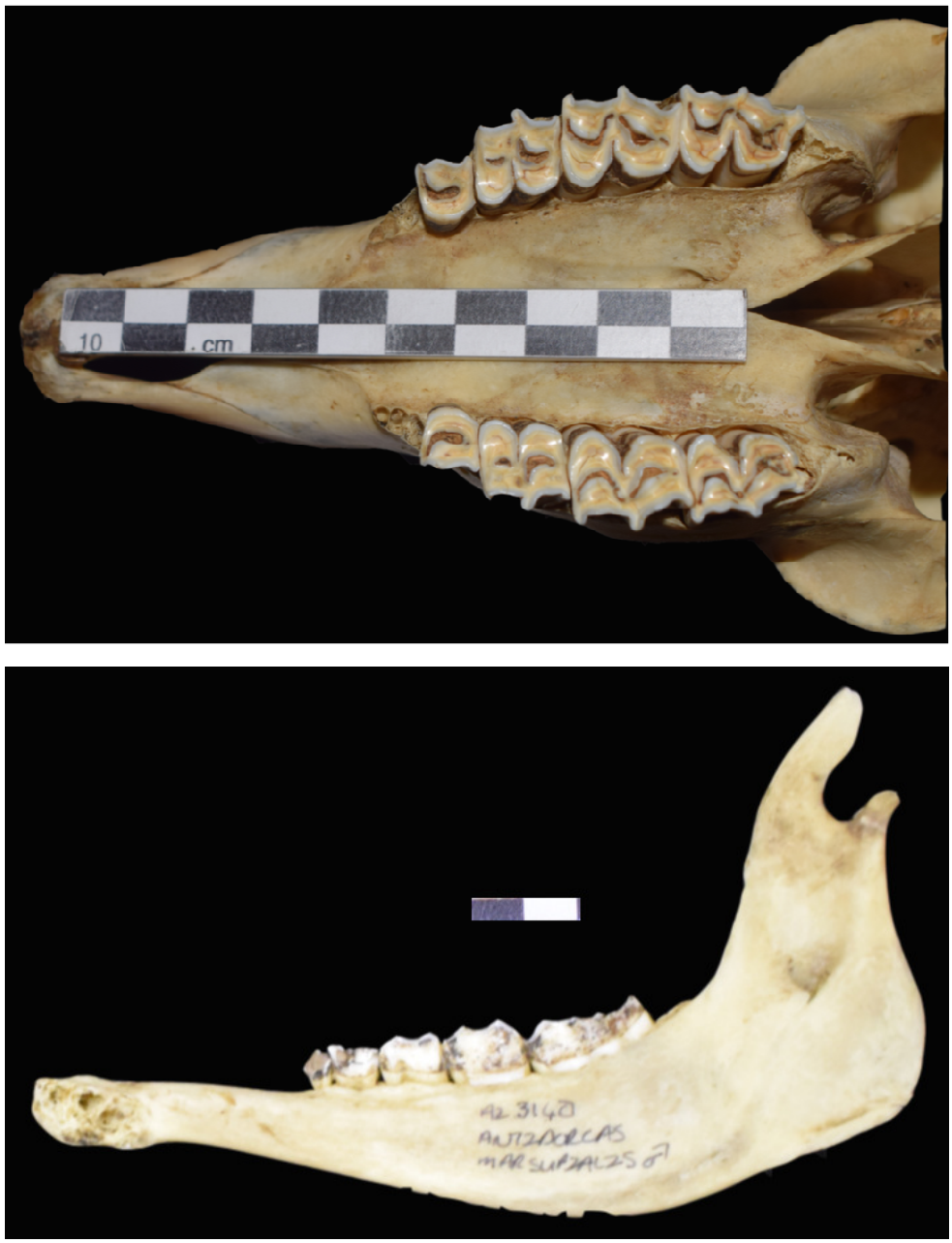


Figure 6.1: Antidorcas marsupialis (male) dentition AZ 3140 (Ditsong Museum of Natural History, Pretoria. Top image shows maxillary dentition in occlusal view, lower image shows right mandibular dentition in lingual view.

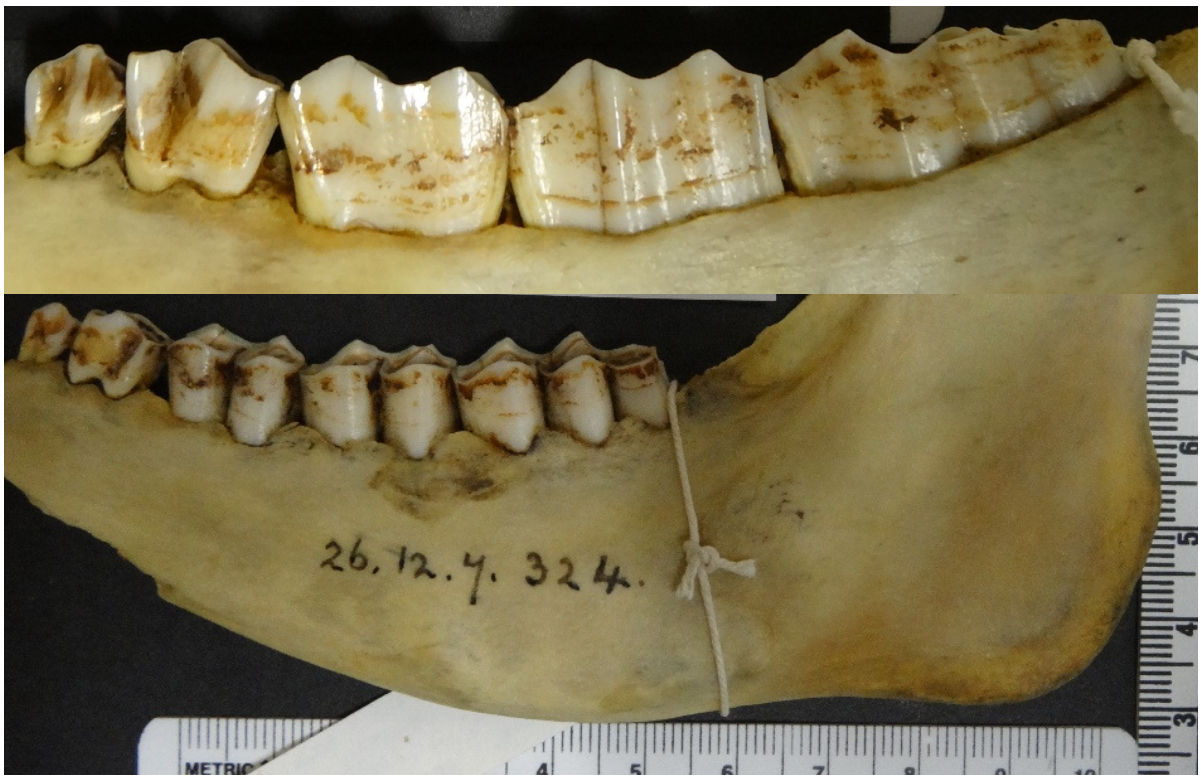


Figure 6.2: Lingual (top) and buccal (bottom) view of modern Antidorcas marsupialis mandibles with lower dentition. NHM. 26.12.7.324

The following tables are indicative of the modern range of variation for *Antidorcas marsupialis*. These tables (Table 6.1-Table 6.15) provide expected variability parameters, to help understand results obtained from fossil *Antidorcas*.

Use-wear (mesowear and microwear) indicates a mixed-feeding diet with a tendency towards browse. No significant differences were found between sub-species for use-wear. The use-wear results for modern *A. marsupialis* from this study (as detailed in this section, below) is supported by published isotope results, indicating a dominance of C_3 plants in the diet e.g. Vogel 1978; Sponheimer et al. 2003; Cerling et al. 2003) are consistent with reported diet of the modern springbok via other study means (e.g. Gagnon and Chew 2000) and field observation (e.g. Bigalke 1972; Nagy and Knight 1994; Skinner and Louw 1996).

6.1.1 Dental Morphology of Modern Springbok

Modern *A. marsupialis* dental specimens of known sub-specific level were tested for significant differences for all methods, other than isotopes (where sub-specific level data was unavailable).

For measurements, tooth types were analysed separately (see chapter 7) BLW and MDL measurements were normally distributed, and no significant differences were found via a one-way ANOVA for any tooth type. The other measurements (CH, OH, TH) were not normally distributed and were subject to non-parametric statistical analysis (although the same significant differences were found via a parametric one-way ANOVA). Significant differences were found for M^1, for crown height between the larger *A .m. hofmeyri* and the smaller, more variable, *A. m. angolensis.* The differences found in occlusal height are between *A. m. marsupialis* and *A. m. angolensis*, and *A. m. hofmeyri* and *A. m. angolensis*.

A. m. angolensis shows more individual variation within the sub-species but mean occlusal height is the tallest of the sub-species.

Because sub-specific level significant differences occur for dental measurements in modern *Antidorcas*, it is anticipated that identifying *A. australis* as a sub-species may be challenging or unachievable from dental measurements alone. Could *A. m. angolensis* for example, show as much/more variation than the difference between *A. australis* and any of the other fossil species, particularly fossil *A. marsupialis*? In which case, *A. australis* should not be identified as a separate species. It does however, highlight the possibility that *A. australis* could show significant differences from *A. marsupialis* for isolated molars even if only sub-specifically taxonomically different.

Potential *A. australis* specimens would ideally need to show significant differences for more than one tooth type across the tooth row (as is the case for the measurements of the different *Antidorcas* fossil species). This would require a collection of toothrows (rather than isolated molars). Additionally, some degree of niche partitioning suggestion via use-wear analysis would encourage confidently suggesting *A. australis* to be regarded as a distinct grouping.

Measurements summaries for M^2 (upper permanent second molar) are provided in the following tables. Measurement acronyms are presented in chapter 4 (Materials and Methods).

Table 6.1: Extant Antidorcas marsupialis M^2 measurement descriptive statistics. (Number of individuals (n), mean, mode, median, minimum, maximum and range) All measurements are given in mm to 1 decimal place.

Descriptive	MDL	BLW	CH	OH	A	B	C	D
N	64	64	64	44	20	20	20	20
Mean	16.0	11.4	10.8	2.9	1.1	0.8	0.71	1.8
Mode	16.4	11.1	11.5	2.7	1.0	0.6	0.6	2.1
Median	16.4	11.6	11.2	2.7	1.1	0.7	0.7	1.7
Minimum	8.3	2.2	1.8	1.4	0.9	0.4	0.6	1.2
Maximum	19.6	14.2	22.0	9.5	1.3	1.1	0.9	2.4
Range	11.3	12.0	20.2	8.1	0.4	0.7	0.3	1.2

Sexual dimorphism

When considering fossil variation, identifying sex of an individual from an isolated molar is almost impossible. By evaluating the level of sexual dimorphism found within modern *Antidorcas marsupialis*, an idea regarding the likely degree of sexual dimorphism in the fossil record can be attained. Where groupings exist in the fossil record, these may be due to sexual dimorphism, and thereby suggest which sex the fossil molar belonged to. Alternatively, these groupings could be due to sub-specific or perhaps population (as the deposits are time-averaged and dental adaptation may have occurred within the timeframe incorporated in the member assemblages) differences within the assemblage.

Modern *Antidorcas* dental measurements showed significant differences between males and females (Table 6.2). Males have consistently larger mean dentition values but there is overlap in their dental size ranges. As shown in Table 6.3, males show significantly larger bucco-lingual widths and enamel thickness (location B, see methods chapter 4, 'Measurements').

Table 6.2: Summary of modern Antidorcas measurements for M^2 (upper permanent second molar) separated according to sex to establish the range of sexual dimorphism present in dentition. MDL=mesio-distal length; BLW= bucco-lingual width; CH= Crown height; OH = occlusal height; A=enamel thickness at location A; B= enamel thickness at location B; C= enamel thickness at location C; D= enamel thickness at location D. Measurements in mm. Means given to 2 decimal places, ranges given to 1 decimal place.

Sex	**N**		**MDL**	**BLW**	**CH**	**N**	**OH**	**N**	**EA**	**EB**	**EC**	**ED**
Male	21	Mean	16.16	12.10	11.64	10	2.54	11	1.07	0.86	0.71	1.95
		Range	14.5-18.2	10.4-13.1	9.0-22.0		1.4-3.9		0.9-1.2	0.4-1.1	0.6-0.9	1.5-2.4
Female	16	Mean	16.16	11.37	10.03	9	4.06	7	1.04	0.59	0.74	1.73
		Range	13.0-22.9	9.4-14.2	1.8-16.0		1.6-9.5		0.9-1.3	0.5-0.7	0.6-0.9	1.5-2.1

Null hypothesis: There are no significant differences in M^2 molar measurements between male and female *Antidorcas marsupialis*.

Table 6.3: Significant differences for Antidorcas marsupialis M^2 across specimens of known sex (i.e. sexual dimorphism in dentition). 'Sig.'=significance.

Null Hypothesis	Test	Sig.	Decision
The distribution of BLW is the same across categories of Sex.	Independent-Samples Mann-Whitney U Test	.008	Reject the null hypothesis.
The distribution of Enamel Thickness (B) is the same across categories of Sex.	Independent-Samples Mann-Whitney U Test	.011	Reject the null hypothesis.

No other measurements showed significant differences and the null hypothesis is retained for these measurements (MDL, CH, OH, EA, EC, ED).

Sub-specific variation

Measurements of second molars from the three recognised sub-species of extant *Antidorcas* were summarised and tested for significant differences.

Table 6.4: Summary of modern Antidorcas measurements for M^2 (upper permanent second molar) separated according to sub-species to establish the range of variation within species present in dentition. MDL=mesio-distal length; BLW= bucco-lingual width; CH= Crown height; OH = occlusal height; Measurements in mm. Means given to 2 decimal places, ranges given to 1 decimal place.

Sub-species	N		MDL	BLW	CH	OH
A.m. marsupialis	49	Mean	16.21	11.61	11.01	2.63
		Range	13.0-22.9	9.4-14.2	4.8-22.0	1.4-3.9
A.m. hofmeyri	8	Mean	17.35	11.84	11.63	2.49
		Range	16.5-18.6	10.8-13.0	10.4-130	1.6-3.4
A.m. angolensis	5	Mean	16.18	11.72	7.10	5.24
		Range	15.6-16.5	10.9-12.2	1.8-11.8	2.1-9.5

A non-parametric kruskal-wallis test with post-hoc Mann-Whitney U pairwise comparisons showed significant differences exist for dentition across sub-species of *A. marsupialis,* when separated by tooth type (Table 6.5). Non-parametric tests were used because the data did not meet the assumption of normal homogeneity of variance to allow parametric statistical analysis. However, the homogeneity of variance was significantly different only for the measurements that showed significant difference across sub-species. It is suggested that these apparent significant differences may actually be an artefact of differential sample sizes.

From this, either Castelló (2016)'s elevation of these sub-species to species level should be viewed as accurate. Alternatively, caution should be advised against differentiating species on dental measurements alone and a conservative approach taken to assessing where speciation occurs from dental morphology in the fossil record.

Table 6.5: Modern Antidorcas sub-specific significant differences in M^2 measurements. All measurements given in mm to 2 decimal places. Mean and range of significantly significant measurement differences are given and detailed in the text below the table. UM1= M^1 upper first molar, UM2= M^2, upper second molar.

Molar	Sub-species	N	Measurement	Mean	Range
UM1	*A. m. marsupialis*	25	**CH**	10.08	3.50-13.30
	A. m. hofmeyri	7		11.91	9.40-13.80
	A. m. angolensis	5		6.60	1.10-11.80
	A. m. marsupialis	25	**OH**	2.01	0.50-3.20
	A. m. hofmeyri	7		1.89	0.50-3.00
	A. m. angolensis	5		5.36	2.20-9.50
UM2	*A. m. marsupialis*	51	**MDL**	15.91	8.30-22.90
	A. m. hofmeyri	8		17.35	16.50-18.60
	A. m. angolensis	5		16.18	15.60-16.50

Table 6.5**: UM1**: **CH** (p=.033) significant difference was between *A. m. hofmeyri* and *A. m. angolensis*. **OH** (p=.042) was significantly different between all species apart from between *A. m. marsupialis* and *A. m. hofmeyri*. **UM2**: **MDL** (p=.011) significant difference was between *A. m. hofmeyri* and *A. m. marsupialis* (p=.003) and *A. m. angolensis* (p=.007).

6.1.2 MESOWEAR

A summary of the differences in mesowear results (for each mesowear variable) from upper, compared to lower dentition, are presented here (Tables 6.6-6.12).

Occlusal relief and cusp shape

Table 6.6: Mesowear occlusal relief and cusp shape relative percentages, separated according to maxillary (upper) and mandibular (lower) dentition (see 'Mesowear' data chapter for further explanation) for modern Antidorcas marsupialis.

Dentition	**N**	**% High**	**% Low**	**% Sharp**	**%Rounded**	**%Blunt**
Upper	107	53	49.53	42.06	47	11
Lower	68	41.18	58.82	25	61.8	13.24

Mesowear Score

Table 6.7: Mesowear scores (occlusal relief and cusp shape variables combined to produce a 'mesowear score', separated according to maxillary (upper) and mandibular (lower) dentition (see 'Mesowear' data chapter for further explanation) for modern Antidorcas marsupialis.

Dentition	N	LB	**% LB**	LR	**% LR**	LS	**% LS**	HB	**% HB**	HR	**% HR**	HS	**% HS**
Upper	107	10	9	31	29	13	12	2	2	19	18	32	29.91
Lower	68	9	13.24	23	33.82	8	11.76	0	0	19	27.94	9	13.24

Occlusal relief with a medium relief category added

Table 6.8: Mesowear occlusal relief scores, with a 'medium' relief category added, separated according to maxillary (upper) and mandibular (lower) dentition (see 'Mesowear' data chapter for further explanation) for modern Antidorcas marsupialis. 'n' shows number of individual specimens.

Dentition	**N**	**High (n)**	**% High**	**Medium (n)**	**% Medium**	**Low (n)**	**% Low**
Upper	105	30	28.57	54	51.43	21	20
Lower	69	11	15.94	38	55.07	20	28.99

New Mesowear scores

Table 6.9: New mesowear scores for modern Antidorcas marsupialis, separated according to maxillary (upper) and mandibular (lower) dentition (see 'Mesowear' data chapter for full explanation of this scoring system).

Dentition	N	Sharp	**% S**	Sharp-Rounded	**% S-R**	Rounded-Sharp	**% R-S**	Rounded	**% R**	Rounded-Blunt	**% R-B**	Blunt-Rounded	**% B-R**	Blunt	**% B**
Upper	105	27	26	17	16	13	12	23	22	14	13	5	5	6	5.71
Lower	69	10	14	8	12	16	23	14	20	10	14	5	7	6	8.70

Table 6.10: Mesowear III Method scores for modern Antidorcas marsupialis (mesowear III/ Inner mesowear scores are only applicable to maxillary (upper) dentition).

N	Mesowear III Score							
	1	**1%**	2	**2%**	3	**3%**	4	**4%**
19	6	31.58	6	31.58	6	31.58	1	5.26

Sexual dimorphism

Table 6.11: Median mesowear variables for modern Antidorcas marsupialis of known sex for maxillary dentition, to establish the sexual dimorphism apparent in dietary behaviour.

	Mesowear score 0-4	**Mesowear score 1-6**	**Relief**	**Cusp shape**	**New relief**	**New cusp shape**	**New score (1-49)**
Male (n=11)							
Median	2	3	1	2	2	4	23
Std. Deviation	1.45	1.83	0.47	0.75	0.54	2.05	12.88
Range	4	5	1	2	2	6	46
Female (n=14)							
Median	3	2	1	2	1.5	5	9
Std. Deviation	1.07	1.27	0.27	0.73	0.65	2.02	14.25
Range	4	5	1	2	2	6	48

Sub-specific variation

Table 6.12: Median mesowear values for maxillary molars of modern Antidorcas marsupialis sub-species, to establish the sub-specific variation apparent in dietary behaviour.

	Mesowear score 0-4	**Mesowear score 1-6**	**Relief**	**Cusp shape**	**New relief**	**New cusp shape**	**New score (1-49)**
A. m marsupialis (n=19)							
Median	3	2	1	2	2	3	17
Range	4	5	1	2	2	6	48
A. m . hofmeyri (n=5)							
Median	2	2	1	2	2	5	18
Range	1	2	0	1	0	3	9
A. m. angolensis (n=1)							
Median	0	3	1	3	2	7	28
Range	x	x	x	x	x	x	x

6.1.3 MICROWEAR (DMTA)

Table 6.13: Summary dental microwear texture parameter statistics. Mean (M), standard deviation (SD) and standard error of the mean (SEM) for modern Antidorcas marsupialis. N=43. Measured in µm. All values given to 2 decimal places.

Asfc			epLsar ($x10^{-3}$)			H*Asfc* 9			H*Asfc* 81			Tfv2			Smc		
M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM
4.10	3.94	0.60	0.00343	0.00170	0.00026	0.54	0.33	0.05	1.02	0.62	0.09	42010.3	11510.9	1755.4	0.19	0.23	0.04
Range: 23.50			Range: 0.00770			Range: 1.44			Range: 2.78			Range: 67583.3			Range: 1.12		

Sexual dimorphism

Table 6.14: Summary dental microwear texture parameter statistics for Antidorcas marsupialis according of known sex, separated to assess dietary sexual dimorphism. Range, mean (M), standard deviation (SD) and standard error of the mean (SEM). Measured in µm. All values given to 2 decimal places.

Male *Antidorcas marsupialis* (n=11)																	
Asfc			epLsar			H*Asfc* 9			H*Asfc* 81			Tfv2			Smc		
M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM
2.70	1.19	0.36	0.00350	0.00149	0.00045	0.54	0.27	0.08	0.75	0.31	0.09	40716.3	7837.6	2363.1	0.22	0.34	0.10
Range: 3.45			Range: 0.00462			Range: 0.93			Range: 0.86			Range: 19460.2			Range: 1.12		
Female *Antidorcas marsupialis* (n=14)																	
Asfc			epLsar			H*Asfc* 9			H*Asfc* 81			Tfv2			Smc		
M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM
2.73	1.54	0.41	0.00383	0.00199	.00053	0.48	0.39	0.10	0.79	0.58	0.15	39217.0	6758.5	1806.3	0.13	0.09	0.02
Range: 5.08			Range: 0.01			Range: 1.44			Range: 2.26			Range: 22478.7			Range: 0.22		

Table 6.14 shows that very little sexual dimorphism is observed in the feeding behaviour, as observed through microwear texture variable, in the modern *Antidorcas marsupialis*. However, there is a considerable range of variation for *Asfc* values for the combined (male and female) values, suggesting dietary variability is prevalent, evident through complexity of enamel surfaces. Unfortunately, sub-species could not be assessed for DMTA variables as sample sizes were too small.

6.1.4 ISOTOPES

Stable carbon isotope values for modern South African *Antidorcas marsupialis* are from published sources. Mean values are given from the references provided.

Table 6.15: Extant Antidorcas marsupialis carbon isotope values (mean $\delta^{13}C$ ‰), their resultant dietary categorisation and the references these values were taken from. (References are detailed further in Appendix A6).

Mean $\delta^{13}C$ (‰)	Diet	Reference
-18.10	Browser	Vogel 1978
-10.10	Browser	Sponheimer et al. 2003
-11.4	Mixed-feeder (browser)	Luyt 2017

Extant *Antidorcas marsupialis* display browse (C_3 vegetation) dominated diets via stable carbon isotope analysis. Luyt 2017 highlights that compared to specialist grazers or browsers, *A. marsupialis* as 'mixed feeders' were the least helpful in deciphering between modern vegetation biomes. In part, this is because they align more closely with obligate browsing isotope values, as evidenced via Table 6.15. However, by appreciating this trend for stable isotope values and by utilising the isotope values alongside the other methods implemented here, mixed feeders can be reliable reflectors of their environment (e.g. Berlioz et al. 2018). Further, although overall depleted $\delta^{13}C$ values may be yielded, the trend of increased/decreased C_3/C_4 consumption should still prevail according to habitat type. Although *A. marsupialis* did not clearly reflect the vegetation composition of each modern vegetation biome through carbon isotope analysis in Luyt's (2017) study, their $\delta^{13}C$ values did adjust according to the biome. Albeit within the range of browsing diets in the actual $\delta^{13}C$ values, a difference was apparent for each vegetation biome and varied to that of either obligate browsers, or obligate grazers. Thereby showing that mixed-feeders do have a role to play as environmental proxies.

SECTION 2: Fossil taxonomic identification and the presence of *Antidorcas australis*

In this chapter, dental specimens that have at some point been tentatively assigned to *A. australis* (e.g. by Vrba 1973) will be scrutinized in an attempt to add to this debate on the taxonomic status of *A. australis*. This chapter will also enable more efficient grouping of specimens taking this research forward. The taxonomic identity of '*A. australis*' is established here to ensure species groupings are accurately made for the following data chapters (chapter 7-10). The potential *A. australis* specimens are evaluated individually for morphological comparisons with the rest of the dataset (of identified *Antidorcas* species) used in this research. Behavioural (dietary) indicators (use-wear and stable isotope analysis) are then used to supplement visual and morphological identifications. Care is taken to avoid circular reasoning of dietary evidence to inform on species taking this research forward. This is achieved by only using the dietary evidence as a supplementary indicator, rather

than conclusive stand-alone evidence, of species identification. If the specimens assigned to *A. australis* show limited differentiation in dental morphological indicators, within the range of variation of modern *Antidorcas* sub-species and this is supported by behavioural (dietary) indicators from *A. marsupialis*, *A. australis* will be taken forward as a sub-species and integrated into the 'fossil *A. marsupialis'* grouping for this research. If considerable variation is apparent, the two will be separated as distinct species/ groups. Since their original classification (Vrba 1973), some of the specimens have since been re-identified (e.g. de Ruiter 2003), and these newer identifications will be considered here, alongside visual taxonomic classifications implemented personally (as detailed below and in chapter 4).

6.2.1 Measurements

No significant difference was found between right- and left-sided molars for any fossil or modern *Antidorcas* species in this study. Therefore, right- and left-sided dentition is grouped together for analysis. 'Fossil *A. marsupialis'* refers to any *A. australis/marsupialis* specimens that have not been previously identified as '*A. australis'* (Vrba 1973) or suspected as being *A. australis* here (not readily identified as another *Antidorcas* species, based on non-metric traits, by the author). [For a full explanation of the measurements used, see chapters 4 'Measurements'].

Table 6.16: Means and standard deviation (SD) of dental volume; MDL (mesio-distal length of M2) and BLW (bucco-lingual width of M2) for each species. All measurements in mm to 2 decimal places.

Species	**N**	**Mean MDL**	**SD**	**Mean BLW**	**SD**
A. recki	60	13.75	1.48	9.97	2.04
A. bondi	84	14.65	0.93	9.67	1.15
***A. marsupialis/australis* (f)**	104	15.32	1.62	11.26	1.60
***A. marsupialis* (m)**	64	16.04	1.91	11.42	1.81
***A. melampus* (m)**	31	16.98	1.35	11.42	1.55

Table 6.17: Mean and standard deviation (SD) of MDL (mesio-distal length of M2) and BLW (bucco-lingual width of M2) for each species (modern Antidorcas marsupialis and Aepyceros melampus), separated according to sex. All measurements in mm to 2 decimal places.

Species	**Sex**	**N**		**MDL**	**BLW**
Antidorcas marsupialis	Female	25	Mean	15.35	10.85
			SD	2.55	2.66
	Male	29	Mean	16.24	11.92
			SD	1.34	0.79
Aepyceros melampus	Female	18	Mean	16.63	11.43
			SD	1.55	1.86
	Male	13	Mean	17.46	11.41
			SD	0.84	1.03

Results: Occlusal area

Potential '*Antidorcas australis*' specimens were plotted against the other *Antidorcas* species molars measured. For each molar BLW x MDL measurements were used to visually assess likely taxonomic identification based on basic morphological parameters (occlusal area) (Figure 6.3-Figure 6.8).

Some of the potential *A. australis* specimens have almost identical measurements to other specimens readily identifiable to species level. Listed below are the specimens identified as *A. australis* in the literature, coupled with the specimens they align with on the scatter plot here for occlusal area (Figure 6.3-Figure 6.8). The specimen they align with and that specimen's species identification is given in the table below.

Table 6.18: 'A. australis' specimens and the Antidorcas species they align most closely with based on morphological measurements. 'Known species' (and their 'known specimen number') specimens have been identified by the author (often supported by published sources, where the specimen has been taxonomically identified). A. marsupialis refers to fossil specimens unless otherwise stated.

Molar	'*A. australis*'	Known species	Known specimen number
M^1	SKX 32887	*A. recki*	KW 9106
	SKX 14250	Modern *A. marsupialis*	NHM.31.2.1.34
			NHM.20.4.27.35
	SKX 29278	*A. marsupialis*	SK 50 0049
M^2	SK 30334	Modern *Antidorcas marsupialis*	Multiple specimens
	SKX 35320		
	SK 3055		
	SKX 35327		
	KA 1111		
M_1	SKX 11602	*A. bondi*	SK7435
M_2	SKX 20143	*A. marsupialis*	SF 548
	SKX 8455a	*A. recki*	KA 1205
			GV 8250
		Modern *A. marsupialis*	NHM.2.12.1.35
			NHM.28.9.11.450
	STS 2076	*A. bondi*	SK 6080
	SK 2310	*A. bondi*	COH 2445
	SKX 28999	*A. bondi*	SK12677
			SK 117
			SF 890(2)
	STS 1944(2)	*Antidorcas* sp	COH 1589
		A. bondi	KA 999
			PV 10724
	KA 964b	*A. bondi*	SK 5354
			STS 1125
			SF 677
	KA 1002	*A. bondi*	SK 10577
M_3	STS 2369	Modern *A. marsupialis*	AZ 3140
	SK 12056	*A. recki*	KW 8152
	KA 964b(2)	*A. bondi*	SK 12669
	KA 1002 (2)	*A. bondi*	SK 10278

In these instances, basic tooth morphology appears indistinguishable from other species and should not be assumed to be a separate (*A. australis*) species. However, this is based on only two linear measurements and can only hint at species similarities rather than proving taxonomy absolutely. Thus, this is used as one piece of evidence alongside many others to

assess each potential *A. australis* specimen analysed in this study (see Table 6.20, Table 6.23).

This may be particularly pertinent for those specimens that align perfectly with more than one species (e.g. SKX 8455a aligns with both *A. recki* and modern *A. marsupialis,* see Figure 6.7) highlighting the range of variation and extent of overlap of measurements prevalent within the genus and perhaps indicative of *A. australis* as a transitional form. Alternatively, the '*A. recki'* specimen may be misidentified and perhaps represents *A. marsupialis/ pre-marsupialis*. Specimens that align to fossil *A. marsupialis* may indicate very little as these might simply not have been considered by other researchers, such as Vrba, and so not previously suggested as being *A. australis*. The degree of overlap of all *Antidorcas* species however (including *A. bondi*, which is more readily visibly identifiable), renders identifying potential *A. australis* from dental occlusal measurements in isolation as challenging.

Similarly, in Figure 6.7, of lower second molars, individuals such as STS 1944 (number 10) and KA 964b (number 11) would strongly suggest being *A. bondi*. Many of the '*A. australis*' specimens have been reassigned to *A. bondi* over the years by various researchers (e.g. de Ruiter 2003).

All other taxonomic assignments from morphology (see Table 6.16-Table 6.17) are suggested based on the closest measurements.

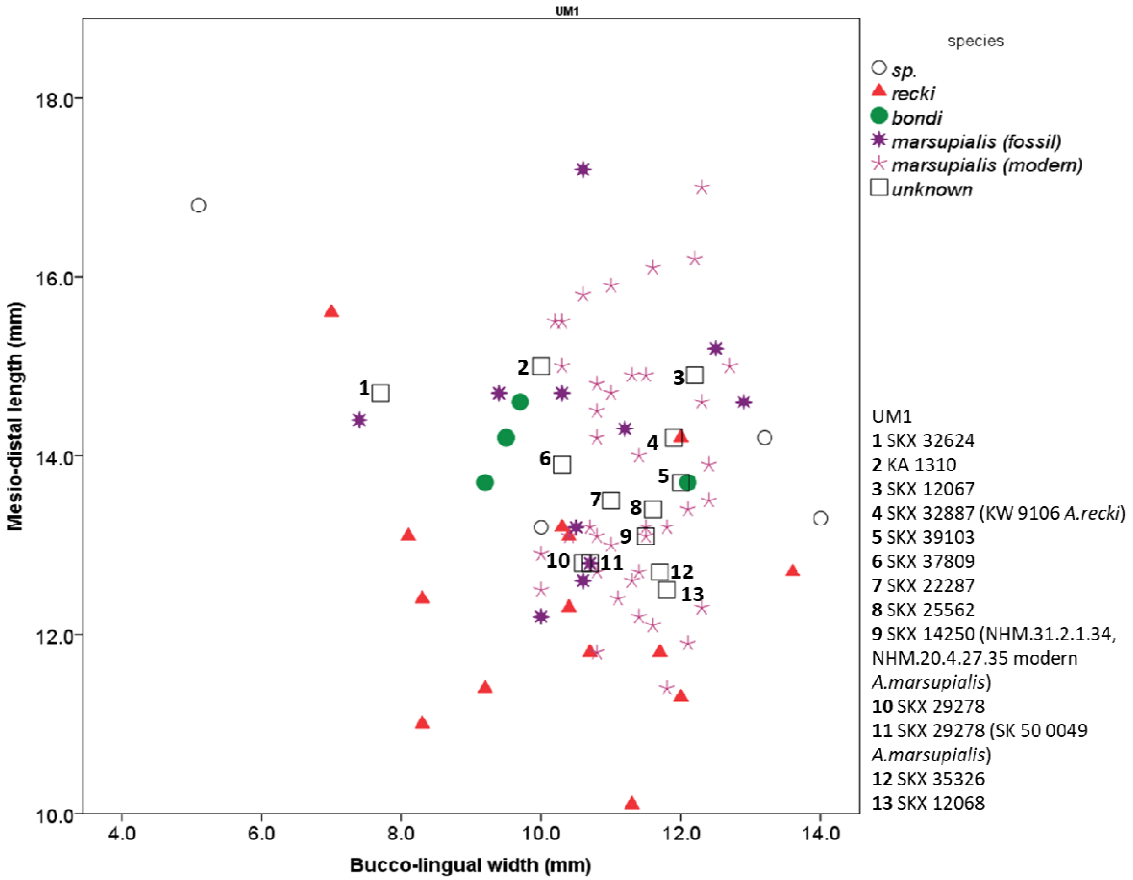


Figure 6.3: Scatter plot for Antidorcas M^1 area (MDLx BLW) of potential A. australis specimens compared to known Antidorcas species. Where unknown species directly map onto the dimensions of known species, the known species is given in brackets next to the unknown species specimen number (specimen number and species).

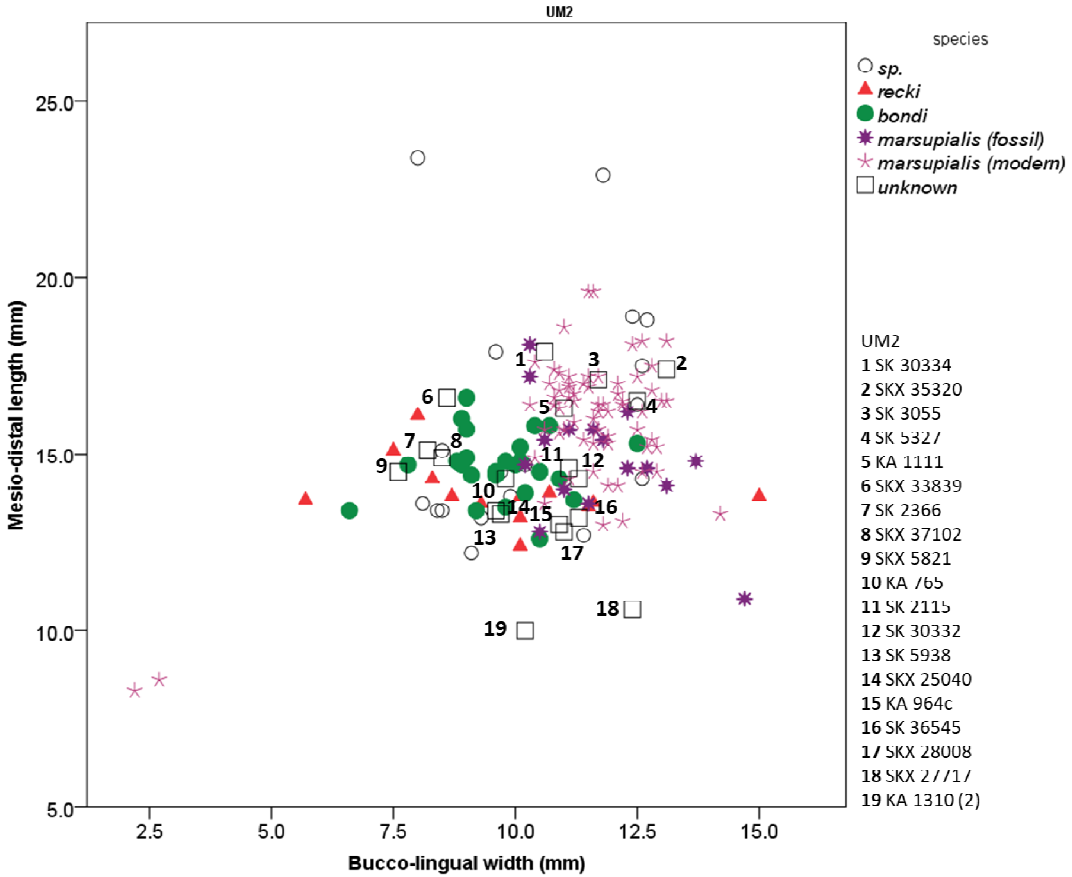


Figure 6.4: Scatter plot for Antidorcas M^2 area (MDLx BLW) of potential A. australis specimens compared to known Antidorcas species. Where unknown species directly map onto the dimensions of known species, the known species is given in brackets next to the unknown species specimen number (specimen number and species).

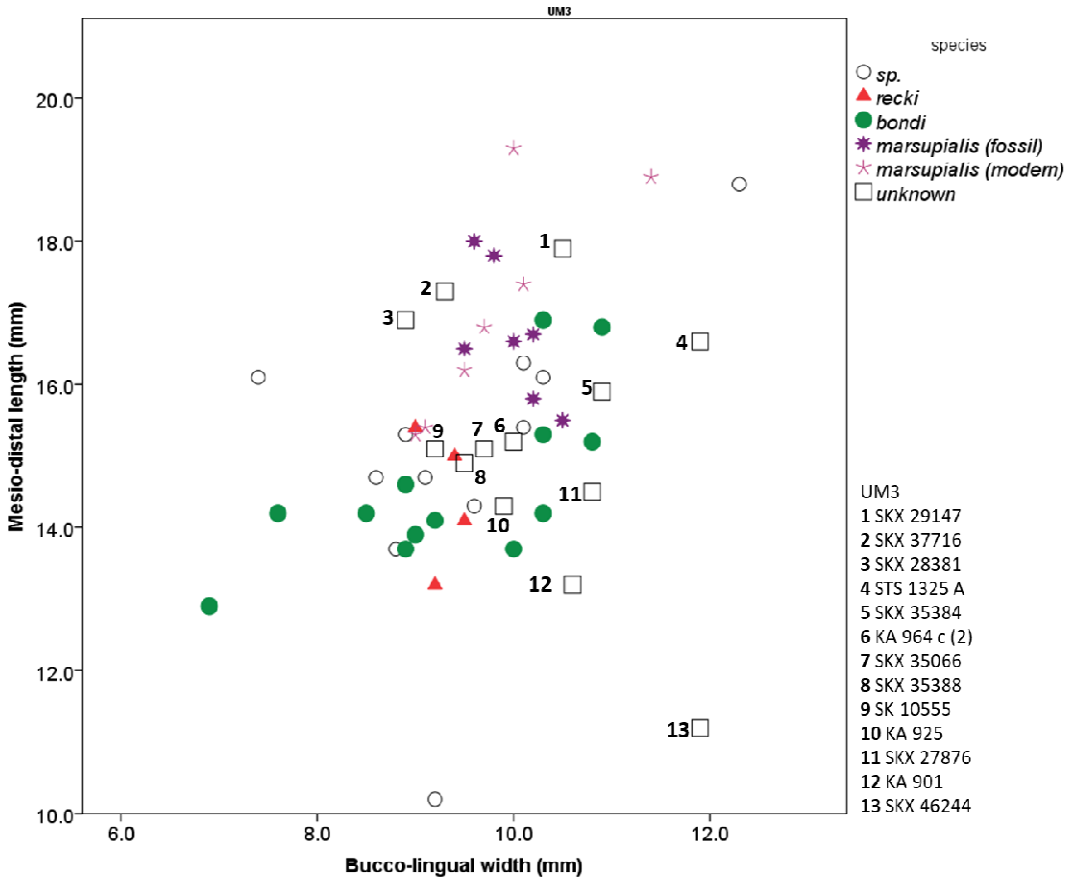


Figure 6.5: Scatter plot for Antidorcas M^3 area (MDLx BLW) of potential A. australis specimens compared to known Antidorcas species. Where unknown species directly map onto the dimensions of known species, the known species is given in brackets next to the unknown species specimen number (specimen number and species).

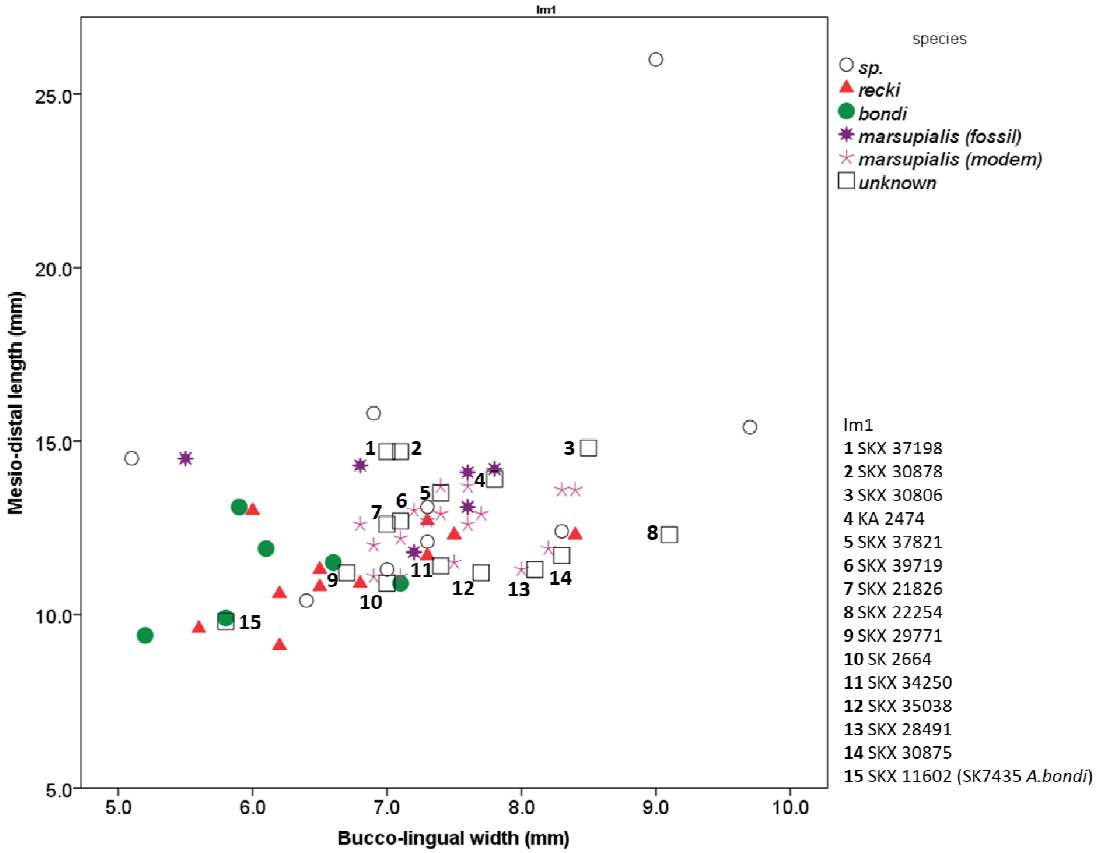


Figure 6.6: Scatter plot for Antidorcas M_1 area (MDLx BLW) of potential A. australis specimens compared to known Antidorcas species. Where unknown species directly map onto the dimensions of known species, the known species is given in brackets next to the unknown species specimen number (specimen number and species).

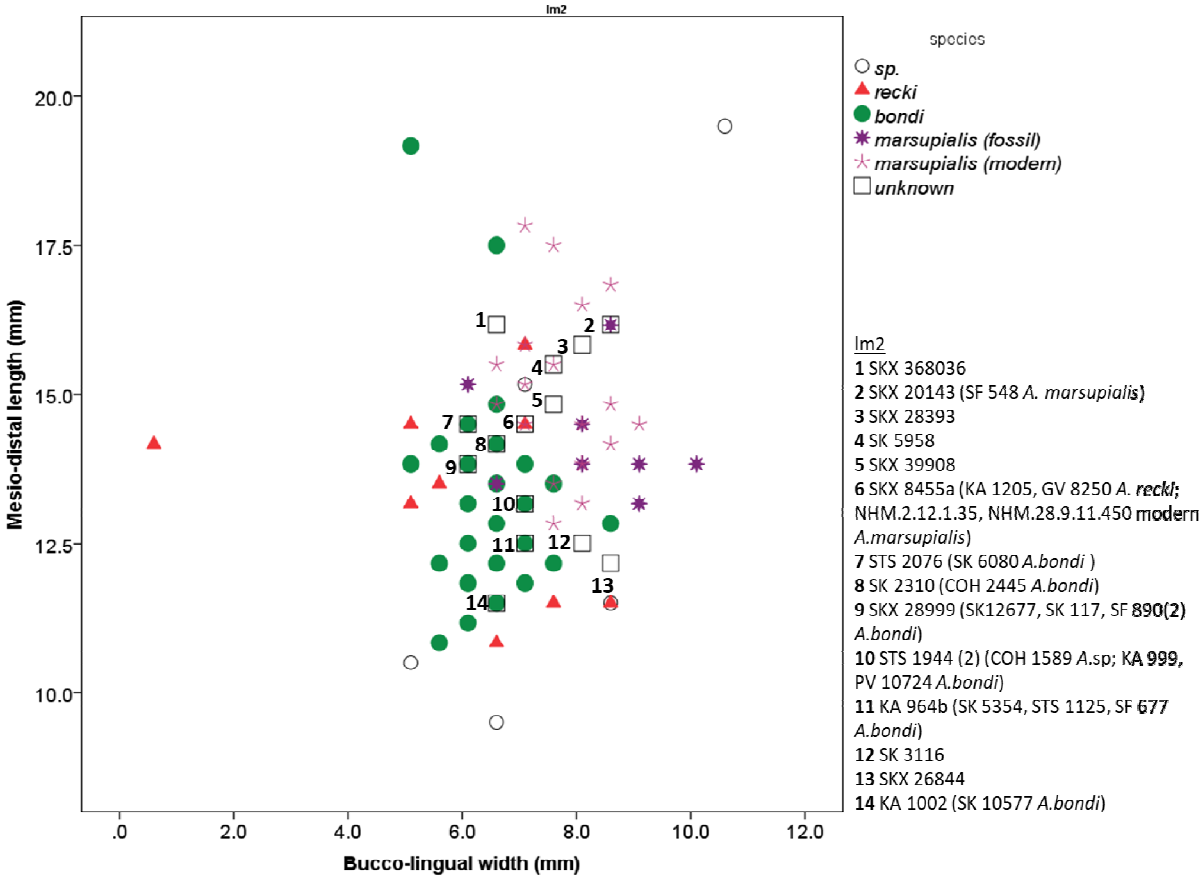


Figure 6.7: Scatter plot for Antidorcas M_2 area (MDLx BLW) of potential A. australis specimens compared to known Antidorcas species. Where unknown species directly map onto the dimensions of known species, the known species is given in brackets next to the unknown species specimen number (specimen number and species).

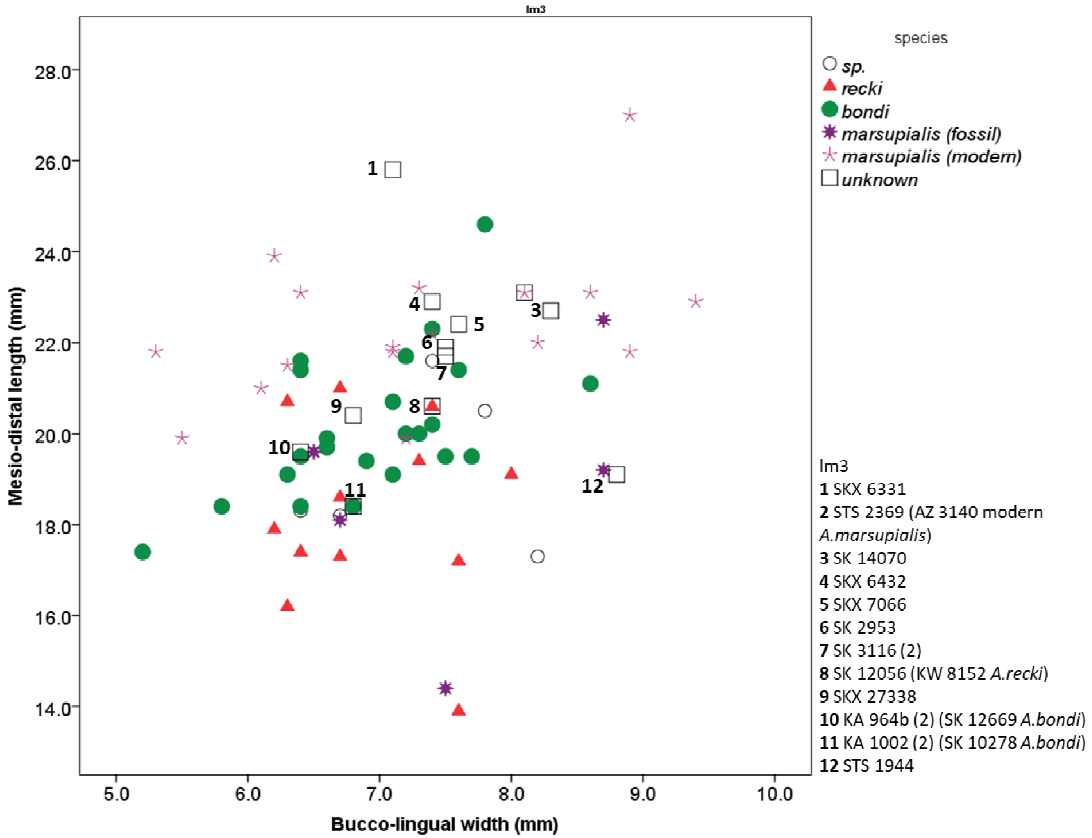


Figure 6.8: Scatter plot for Antidorcas M_3 area (MDLx BLW) of potential A. australis specimens compared to known Antidorcas species. Where unknown species directly map onto the dimensions of known species, the known species is given in brackets next to the unknown species specimen number (specimen number and species).

Results: Enamel Thickness

The same scatter plots (as for linear metrics) were created using enamel thickness measurements. As no significant difference was found between enamel thickness measurements for locations A-C (see 'Measurements' chapter for location of these measurements) for any particular *Antidorcas* species, Enamel A measurements (representing the outer enamel for locations A-C as a proxy for the outer enamel for the entire tooth) were plotted against Enamel D (the mesostyle) measurements (Figure 6.9-Figure 6.11). Enamel thickness at location 'D' is only present in (and therefore, measured on) upper molars.

Based on enamel thickness, some '*A. australis*' specimens had identical (or very similar) measurements to other *Antidorcas* species (Figure 6.9-Figure 6.11). These specimens are listed below, coupled with the species and specimen number (given in brackets) their enamel thickness measurements most closely resemble. This evidence supports these particular specimens as belonging to the same species as those their enamel thickness measurements align with most (Table 6.20 'e' specimens).

Table 6.19: 'A. australis' specimens and the Antidorcas species they align most closely with based on enamel thickness. 'Known species' specimens (specimen number included here as 'known specimen number') have been identified by the author (often supported by published sources, where the specimen has been taxonomically identified). A. marsupialis refers to fossil specimens unless otherwise stated.

Molar	'*A. australis*'	Known species	Known specimen number
M^2	SKX 35320	*Antidorcas* sp	SK 5938
	KA 1111	*A. bondi*	PV 21589
	KA 964c	*A. bondi*	PV 10703
		Modern *A. marsupialis*	AZ 3140
	SKX 35327	*A. bondi*	SKX 52703
	SKX 30332	*A. marsupialis*	SKX 36544
		Modern *A. marsupialis*	AZ 2437
M^3	KA 964c (2)	*A. bondi*	PV 14545
	SKX 35066	*A. marsupialis*	SKX 10703
	SKX 35384	*A. recki*	KA 1639
	SKX 28381	*Antidorcas* sp	COH 1740

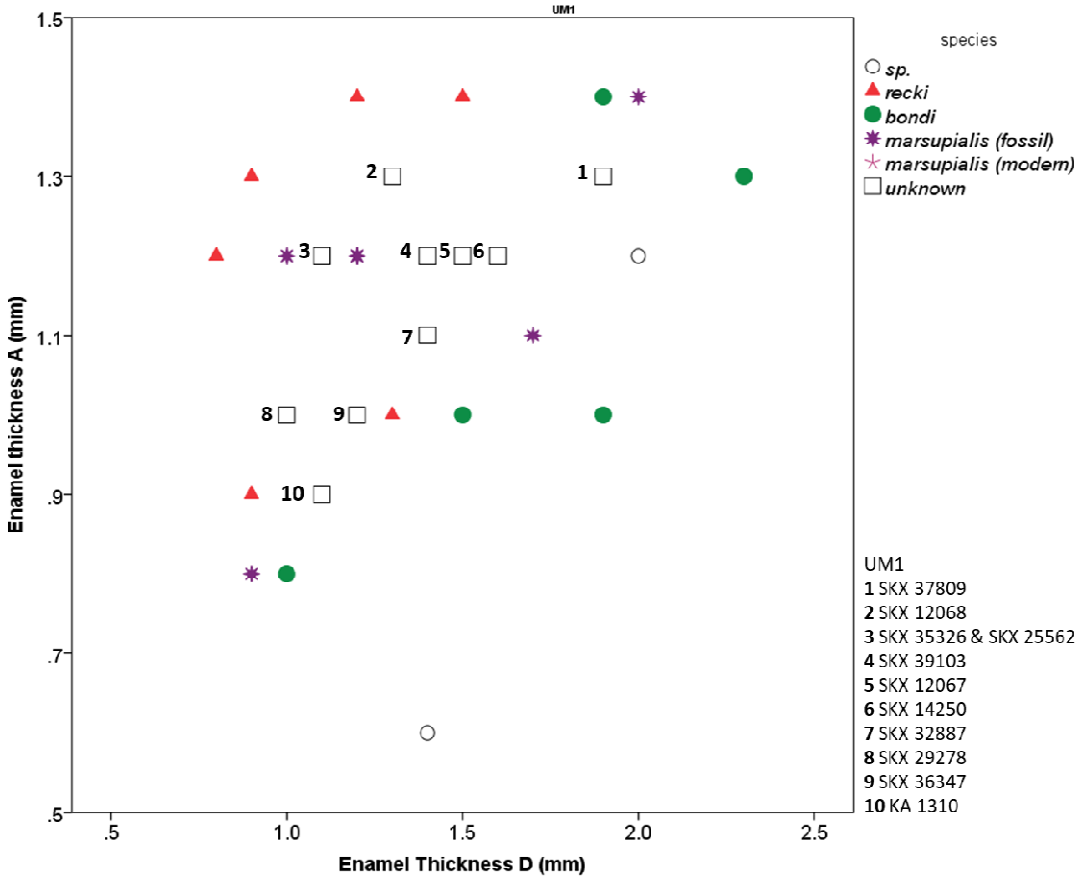


Figure 6.9: Scatter plot for Antidorcas M^1 of potential A. australis specimens enamel thickness A (lingual enamel facet) on the Y axis and D (mesostyle) on the X axis, compared to known Antidorcas species.

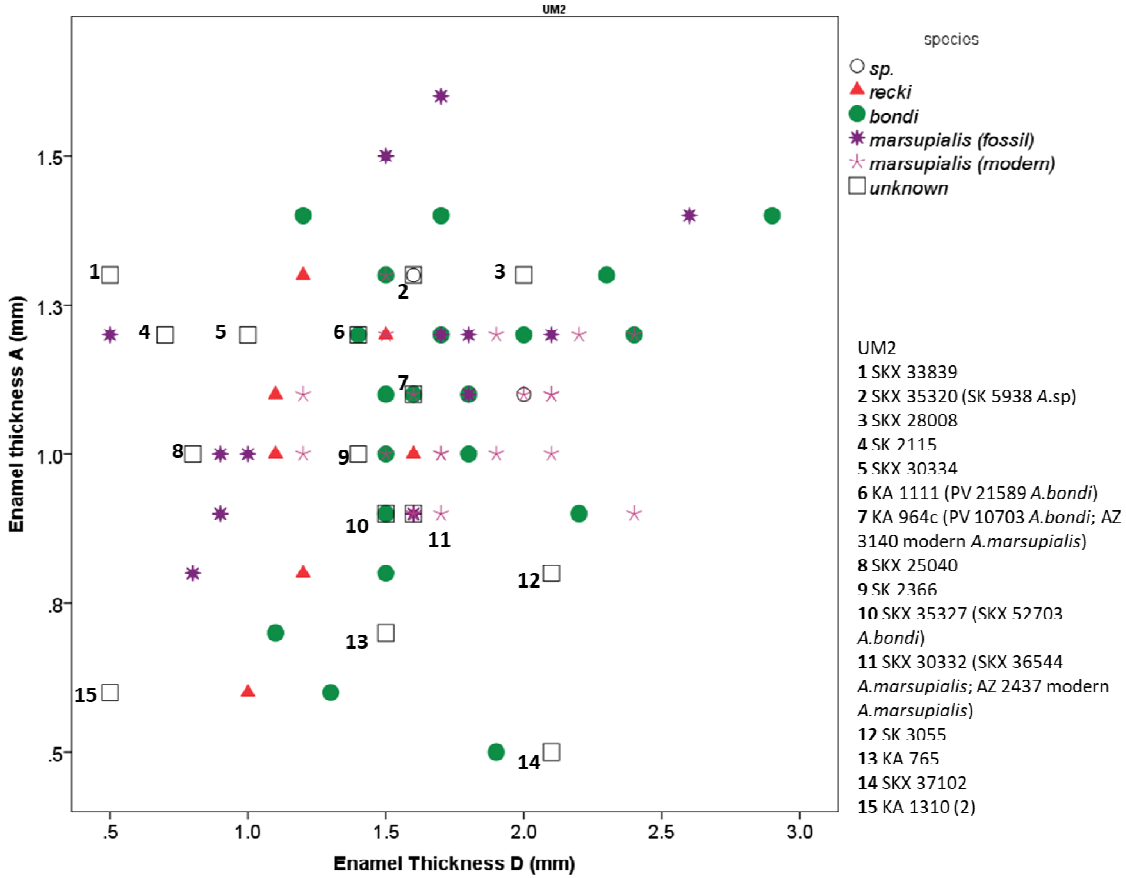


Figure 6.10: Scatter plot for Antidorcas M^2 of potential A. australis specimens enamel thickness A (lingual enamel facet) on the Y axis and D (mesostyle) on the X axis, compared to known Antidorcas species.

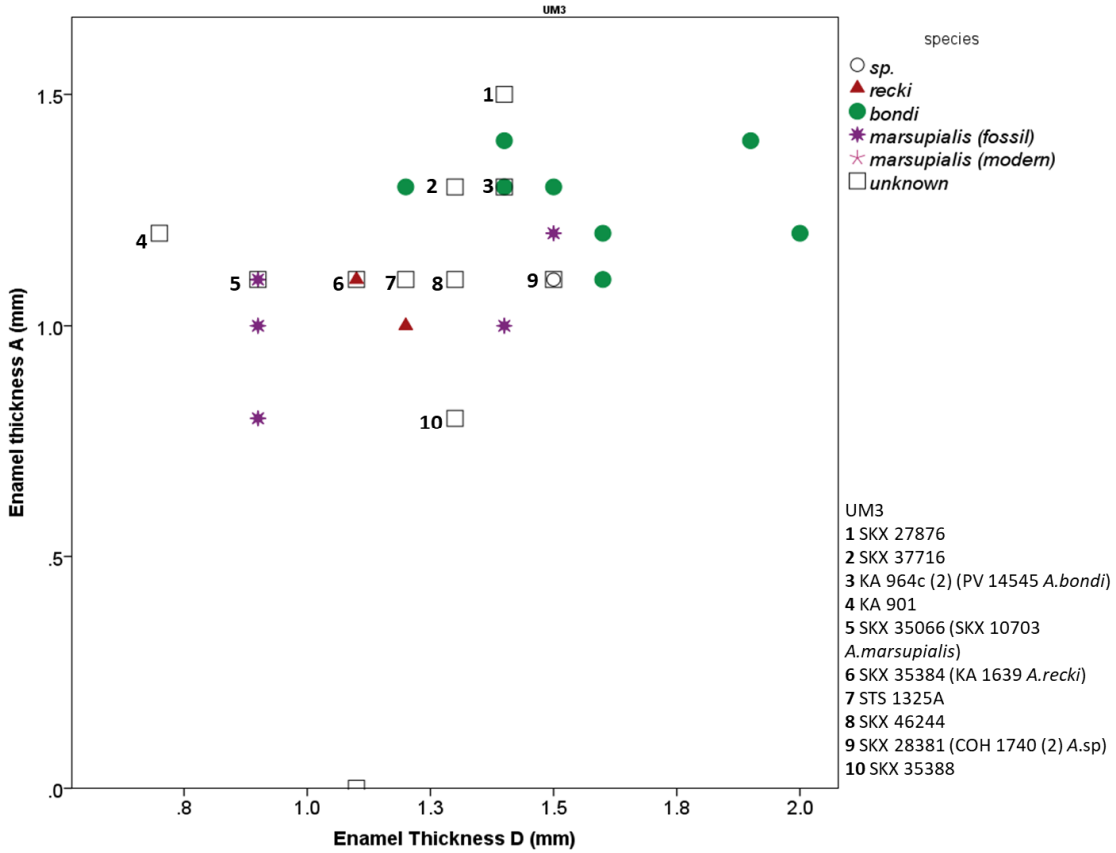


Figure 6.11: Scatter plot for Antidorcas M^3 of potential A. australis specimens enamel thickness A (lingual enamel facet) on the Y axis and D (mesostyle) on the X axis, compared to known Antidorcas species.

*Table 6.20: Table of specimens for taxonomic identification. Morphological taxonomic identifications are based on linear morphological measurements and enamel thickness. *Where specimens are closest to other fossil A. marsupialis, this could be indicative of both being A. australis or A. marsupialis. If occlusal area measurement taxonomic identification indicators differ from those from enamel thickness, (e) indicates where identification is based on enamel thickness, both are quoted in this instance. If the dimension measurements are in agreement for taxonomic identification with the enamel thickness measurements, only one species is presented, with the addition of an '(e)' to show this has the support of both occlusal area dimensions and enamel thickness. Where no specific species aligns more closely than any other based on morphological measurements, 'sp.' is given. 'DFA' indicates these species assignments are a result of the discriminant function analysis (as discussed below).*

Site and Member	**Specimen Number**	**Tooth type**	**Tooth Measured**	**Visual taxonomic ID**	**Morphological taxonomic ID**
Swartkrans Member 1 LB	SKX 5821	Isolated permanent upper tooth	RUM2	*A. australis/marsupialis*	sp.
	SKX 12067	Isolated permanent upper tooth	RUM1	*A. australis/marsupialis*	sp.
	SKX 12068	Isolated permanent upper tooth	RUM1	*A. recki*	sp.
	SKX 14250	Isolated permanent upper tooth	RUM1	*A. australis/marsupialis*	*A. marsupialis*
	SKX 11602	Isolated permanent lower tooth	LLM1	*A. bondi*	*A. bondi****
	SKX 8455a	Isolated permanent lower tooth	LLM2	*A. australis/marsupialis*	*A. marsupialis; A. recki*
	SKX 6331	Isolated permanent lower tooth	LLM3	*A. australis/marsupialis*	sp.
	SKX 6432	Isolated permanent lower tooth	LLM3	*A. australis/marsupialis*	sp.
	SKX 7066	Isolated permanent lower tooth	RLM3	*A. australis/marsupialis*	sp.
Swartkrans Member 2	SK 1055	Isolated permanent upper tooth	LUM3	*A.*cf.*bondi*	sp.
	SK 3055	Right maxilla P4-M3	RUM2	*A. australis/marsupialis*	*A. marsupialis*
	SK 12056	Left mandible fragment, M3	LLM3	*A. recki*	*A. recki*
	SK 5958	Right mandible fragment, M1-M2	RLM2	*A. bondi*	*A. marsupialis*
	SK 3116	Right mandible fragment, M2-M3	RLM2&3	*A. recki*	sp.

Site and Member	Specimen Number	Tooth type	Tooth Measured	Visual taxonomic ID	Morphological taxonomic ID
	SK 2366	Right maxilla fragment, M1-M2	RUM2	*A. bondi*	*A. bondi*^{DFA}
	SK 2115	Left maxilla, P4-M3	LUM2	*Antidorcas* sp.	sp.
	SK 2953	Right mandible fragment, M3	RLM3	*Antidorcas* sp.	sp.
	SK 14070	Left mandible fragment, M3	LLM3	*Antidorcas* sp.	sp.
	SK 2664	Left mandible fragment, P4-M1	LLM1	*Antidorcas* sp.	sp.
Swartkrans Member 3 Swartkrans Member 3	SKX 32176	Mandible piece	RLM1	*A. australis/marsupialis*	sp.
	SKX 21826+21834+21835	Mandible piece	LLM1	*A. australis/marsupialis*	sp.
	SKX 28008	Isolated permanent upper tooth	LUM2	*A. australis/marsupialis*	sp.
	SKX 29147	Isolated permanent upper tooth	RUM3	*A. australis/marsupialis*	sp.
	SKX 29278	Isolated permanent upper tooth	RUM1	*A. australis/marsupialis*	**A. marsupialis*
	SKX 46244	Isolated permanent upper tooth	RUM3	*A. recki*	sp.
	SKX 37809	Isolated permanent upper tooth	RUM1	*A. australis/marsupialis*	sp.
	SKX 36347	Isolated permanent upper tooth	RUM1	*A. australis/marsupialis*	sp.
	SKX 32887	Isolated permanent upper tooth	LUM1	*A. recki*	*A. recki*
	SKX 27876	Isolated permanent upper tooth	RUM3	*A. australis/marsupialis*	sp.
	SKX 27717	Isolated permanent upper tooth	RUM2	*A. recki*	sp.
	SKX 35320	Isolated permanent upper tooth	RUM2	*A. australis/marsupialis*	*A. marsupialis*
	SKX 30334	Isolated permanent upper tooth	RUM2	*A. australis/marsupialis*	*A. marsupialis*

Site and Member	Specimen Number	Tooth type	Tooth Measured	Visual taxonomic ID	Morphological taxonomic ID
	SKX 30332	Isolated permanent upper tooth	RUM2	*A. australis/marsupialis*	*A. marsupialis*
	SKX 20143	Isolated permanent upper tooth	LLM2	*A. australis/marsupialis*	*A. marsupialis**
	SKX 37716	Isolated permanent upper tooth	RUM3	*A. australis/marsupialis*	sp.
	SKX 35066	Isolated permanent upper tooth	RUM3	*A. australis/marsupialis*	*A. marsupialis**
	SKX 35326	Isolated permanent upper tooth	LUM1	*A. australis/marsupialis*	sp.
	SKX 25562	Isolated permanent upper tooth	LUM1	*A. australis/marsupialis*	sp.
	SKX 36545	Isolated permanent upper tooth	LUM2	*A. australis/marsupialis*	sp.
	SKX 35327	Isolated permanent upper tooth	LUM2	*A. australis/marsupialis*	*A. marsupialis; A. bondi* (e)
	SKX 33839	Isolated permanent upper tooth	LUM2	*A. australis/marsupialis*	sp.
	SKX 28381	Isolated permanent upper tooth	LUM3	*A. australis/marsupialis*	sp.
	SKX 35388	Isolated permanent upper tooth	LUM3	*A. australis/marsupialis*	sp.
	SKX 35384	Isolated permanent upper tooth	LUM3	*A. australis/marsupialis*	*A. recki*
	SKX 37102	Isolated permanent upper tooth	RUM2	*A. australis/marsupialis*	sp.
	SKX 32624	Isolated permanent upper tooth	LUM1	*A. australis/marsupialis*	sp.
	SKX 22287	Isolated permanent upper tooth	RUM1	*A. australis/marsupialis*	sp.
Swartkrans Member 3	SKX 25040	Isolated permanent upper tooth	LUM2	*A. recki*	sp.
	SKX 39103	Isolated permanent upper tooth	RUM1	*A. recki*	sp.
	SKX 39611	Isolated permanent upper tooth	RUM1	*A. australis/marsupialis*	sp.
	SKX 39719	Isolated permanent upper tooth	RLM1	*A. australis/marsupialis*	sp.
	SKX 28491	Isolated permanent lower tooth	LLM1	*A. recki*	sp.

Site and Member	Specimen Number	Tooth type	Tooth Measured	Visual taxonomic ID	Morphological taxonomic ID
	SKX 30875	Isolated permanent lower tooth	LLM1	*A. recki*	sp.
	SKX 29771	Isolated permanent lower tooth	LLM1	*A. recki*	sp.
	SKX 26844	Isolated permanent lower tooth	RLM2	*A. australis/marsupialis*	sp.
	SKX 28999	Isolated permanent lower tooth	LLM2	*A. australis/marsupialis*	*A. bondi*
	SKX 37821	Isolated permanent lower tooth	RLM1	*A. australis/marsupialis*	sp.
	SKX 28393	Isolated permanent lower tooth	LLM2	*A. australis/marsupialis*	sp.
	SKX 39908	Isolated permanent lower tooth	RLM2	*A. australis/marsupialis*	sp.
	SKX 38594	Isolated permanent lower tooth	RLM3	*A. australis/marsupialis*	sp.
	SKX 37198	Isolated permanent lower tooth	LLM1	*A. australis/marsupialis*	sp.
	SKX 35038	Isolated permanent lower tooth	LLM1	*A. recki*	sp.
	SKX 34250	Isolated permanent lower tooth	LLM1	*Oreotragus major***	sp.
	SKX 30878	Isolated permanent lower tooth	LLM1	*A. australis/marsupialis*	sp.
	SKX 29420	Isolated permanent lower tooth	LLM2	*A. australis/marsupialis*	sp.
	SKX 30806	Isolated permanent lower tooth	RLM1	*A. australis/marsupialis*	sp.
	SKX 22254	Isolated permanent lower tooth	RLM1	*A. recki*	sp.
	SKX 27338	Isolated permanent lower tooth	RLM3	*A. australis/marsupialis*	sp.
Swartkrans Member 3	SKX 36803b	Isolated permanent lower tooth	LLM2	*A. australis/marsupialis*	sp.
Kromdraai A	KA 901	Left maxilla; P2-M3	LUM3	*A. recki*	sp.
	KA 964b&c	Left hemimandible M1-M3	LLM2&3 LUM2&3	*A. recki*	****A. bondi; A. marsupialis (e)*

Site and Member	Specimen Number	Tooth type	Tooth Measured	Visual taxonomic ID	Morphological taxonomic ID
	KA 925	Left upper M3	RUM3	*A. recki*	sp.
	KA 765	Left maxilla frag, M1-2	LUM2	*A. recki*	*A. recki*^{DFA}
	KA 1111	Left maxilla frag, P2-M2	LUM2	*A. recki*	*A. marsupialis; A. bondi* (e)
	KA 1310	Right maxilla, (B) M1-2	RUM1&2	*A. recki*	sp.
	KA 2474	Left mandible P4-M2	LLM1	*A. recki*	sp.
	KA 1002	Left hemimandible P3-M3	LLM2&3	*A. recki*	*A. bondi*
Sterkfontein Member 4	STS 1325 A	Right upper M2	RUM3	*A. recki*	sp.
	STS 2369	Right mandible P3-M2	RLM3	*A. recki*	*A. marsupialis*
	STS 2076	Left mandible frag, M1-M3	LLM2	*A. recki*	*A. bondi*
	STS 1944	Left mandible frag, M2-M3	LLM2&3	*A. recki*	*A. bondi*
	S94-6871	Right mand. Frag., M1-2	RLM2	*A. australis/marsupialis*	sp.

**SKX 32704 also preliminarily visually identified as cf. *Oreotragus major* (an extinct form of klipspringer with very similar dental morphology to *Antidorcas*). However, morphometrically, this specimen lies in the middle of the other *Antidorcas* M^1 dentition (see Figure 6.3, UM1). Where specimens were measured on 2016 and 2017 data collection trips, 2017 measurements were chosen for this purpose (all measurements fell within the acceptable intra-observer error margin, as established in the Methods section, see chapter 4 and 7). ***SKX 11602 was broken, rendering its mesio-distal length relatively unusable, the present MDL (9.8 mm) was included for the purpose of showing this point on the taxonomic association scatter plots but this point/tooth would have had greater mesio-distal length prior to breakage. ****KA 964B lower M2 and M3 aligned most with *A. bondi*, the enamel thickness of KA 964c with *A. bondi* for the lower M2 and with *A. bondi* and modern *A. marsupialis* for the lower M3.

Individual Taxonomy Discrepancies

The majority of specimens are represented by isolated molars. However, there are a few specimens represented by a toothrow, or more than one molar. For these specimens, measurement-based taxonomic identification indicators are used for each tooth as if they were isolated molars, to ensure consistency.

These individuals (SK 3116, KA 964b & c, KA 1310, KA 1002, STS 1944) were examined to check the taxonomic identifications are consistent across the toothrow. It was found that all taxonomic identifications, from each method implemented, were consistent across the toothrow.

Discriminant Function Analysis

UM2 specimens were subject to a discriminant function analysis, the predictor variables from which could then be carried forward for further DFAs on other molars.

Using the primary measurements that may be expected to be indicative of species, i.e. MDL and BLW, 2 discriminant functions were created and 63% of individuals were correctly classified to species, according to original taxonomic assignments input into this model.

Table 6.21: Discriminant function analysis for UM2 main measurement predictor variables. A. Eigenvalues; B. Wilks' Lambda; C. standardised canonical discriminant function coefficients; D. classification results.

A) Summary of canonical discriminant functions: Eigenvalues

Function	**Eigenvalue**	**% of Variance**	**Cumulative %**	**Canonical correlation**
1	.319	78.9	78.9	.492
2	.085	21.1	100.0	.280

B) Wilks' Lambda

Test of Function(s)	**Wilks' Lambda**	**Chi-Square**	**df**	**Significance**
1 through 2	.699	41.246	6	.000
2	.922	9.397	2	.009

C) Standardised canonical discriminant function coefficients

	Function	
	1	**2**
Mesio-distal length	.514	.925
Bucco-lingual width	.706	-.789

D) Classification results

Species			**Predicted group membership**				
			recki	***bondi***	***marsupialis (fossil)***	**marsupialis (modern)**	**Total**
Original	Count	***recki***	6	4	3	0	13
		bondi	5	15	2	2	24
		marsupialis (fossil)	1	1	8	6	16
		marsupialis (modern)	3	1	16	46	66
		ungrouped	12	7	6	12	37
	%	***recki***	46.2	30.8	23.1	.0	100.0
		bondi	20.8	62.5	8.3	8.3	100.0
		Marsupialis (fossil)	6.3	6.3	50.0	37.5	100.0
		marsupialis (modern)	4.5	1.5	24.2	69.7	100.0
		ungrouped	32.4	18.9	16.2	32.4	100.0

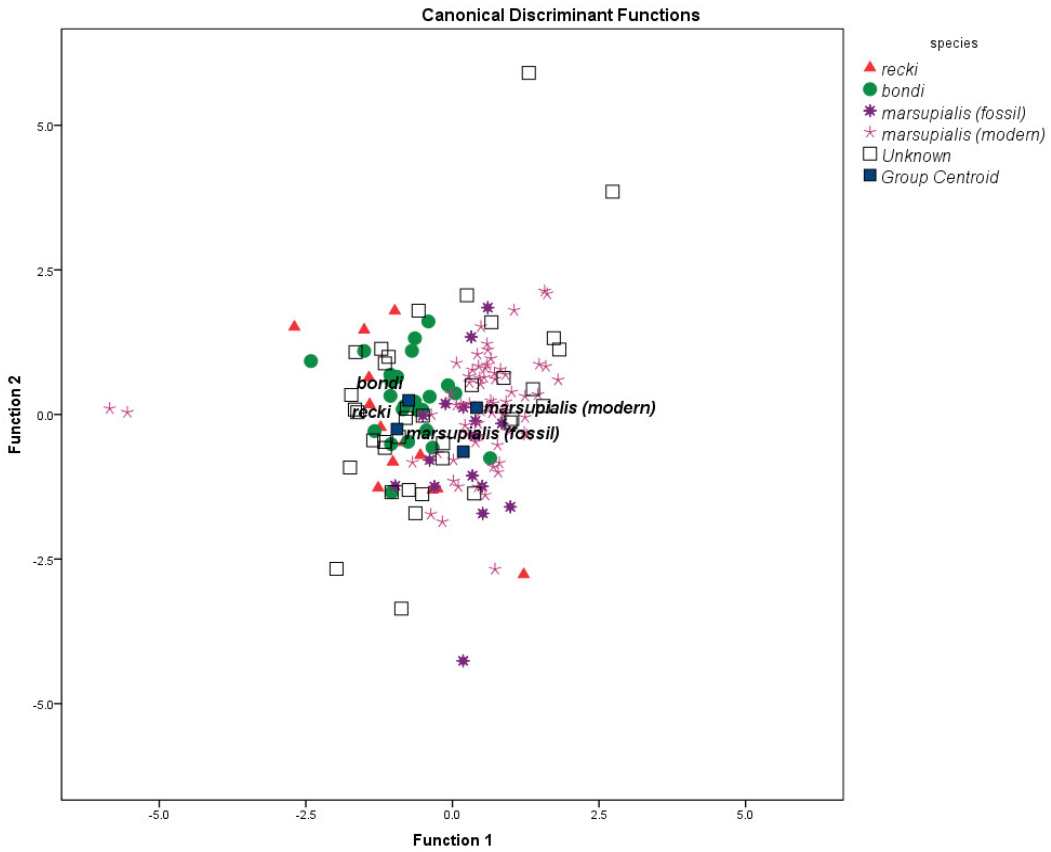


Figure 6.12: Taxonomic assignments using all measurement variables as predictor variables were classified via a discriminant function analysis as being 63% accurate for upper second molars (M^2).

When using all measurements, 100% of original groups were classified correctly in the following DFA. Through the DFA, it was found that cusp height and enamel thickness C were not sufficient species predictor variables and were not used in the analysis, 2 discriminant functions were created.

Table 6.22: Discriminant function analysis results on UM2 using all measurements. A. Eigenvalues; B. Wilks' Lambda; C. standardised canonical discriminant function coefficients; D. classification results.

A) Summary of canonical discriminant functions: Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical correlation
1	72.454	89.0	89.0	.993
2	8.961	11.0	100.0	.948

B) Wilks' Lambda

Test of Function(s)	Wilks' Lambda	Chi-Square	df	Significance
1 through 2	.001	247.324	16	.000
2	.100	86.200	7	.000

C) Standardised canonical discriminant function coefficients

	Function	
	1	**2**
Mesio-distal length	7.033 .884	7.033 .884
Bucco-lingual width	-2.639 -1.307	-2.639 -1.307
Crown height	3.395 1.313	3.395 1.313
Overall height	-5.926 -.368	-5.926 -.368
Enamel Thickness A	-7.171 -1.223	-7.171 -1.223
Enamel Thickness B	2.549 2.028	2.549 2.028
Enamel Thickness D	-5.041 -2.904	-5.041 -2.904
Enamel thickness	8.703 2.413	8.703 2.413

D) Classification results

Species			Predicted group membership			
			recki	***bondi***	***marsupialis/australis***	**Total**
Original	Count	***recki***	20	0	0	20
		bondi	0	16	0	16
		marsupialis/ australis	0	0	8	8
		ungrouped	0	4	0	4
	%	***recki***	100.0		.0	100.0
		bondi	.0	100.0	.0	100.0
		marsupialis/ australis	.0	.0	100.0	100.0
		ungrouped	.0	100.0	.0	100.0

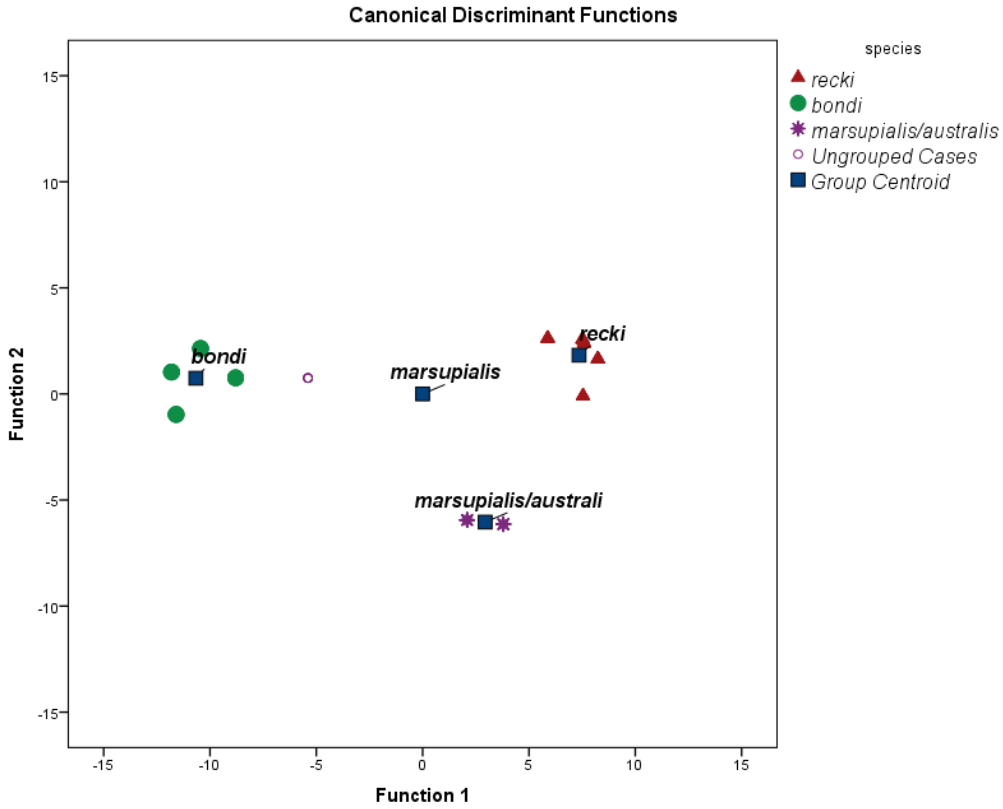


Figure 6.13: Canonical discriminant function of Antidorcas, based on molar measurements and their range of variation of each species, 100% of the original groups were classified correctly.

A discriminant function analysis (DFA) was used to predict the likelihood of potential *A. australis* specimens belonging to another species of *Antidorcas* (Figure 6.12, Figure 6.13). The model was based on measurements of the M^2 BLW and MDL of *A. recki*, *A. bondi*, fossil *A. marsupialis* and modern *A. marsupialis,* with an accuracy of 63%. The '*A. australis*' outliers seen here do not fit easily with any of the other species, perhaps indicating a separate species. However, all other fossil and modern *Antidorcas* specimens tend to overlap considerably, therefore even if another species of *Antidorcas* (such as *A. australis*) were present, one might expect to have at least some degree of overlap.

Although enamel thickness is one of the characteristic features used to distinguish between *Antidorcas* species, with *A. bondi* having thicker enamel (particularly around central cavities on the occlusal surface), only enamel measured at point C (see chapter 4, Figure 4.15) was a good predictor variable. Based on enamel thickness measurements, accuracy of

species assignments is only 34%. In spite of this low accuracy level, enamel thickness for *A. bondi* is shown to be as predicted relative to the overall tooth dimensions. Therefore, another DFA for all predictor variables was conducted. In this case, the model is only 40% accurate at predicting each species overall, other than *A. bondi* which is accurately predicted with 79% accuracy.

A DFA using all measurements taken as predictor variables returns a model with 66% accuracy, predicting with 71% *A. recki* and *A. bondi* with 93% accuracy. This analysis includes overall height (applicable only to isolated molars, so does not include modern *A. marsupialis* where all specimens were *in situ* in the jaw) and enamel thickness measurements B and D. These levels of accuracy appear reasonable for palaeoecological models but undoubtedly there is a margin for error with these models. They do however allow a good starting point for potential species identification, for each to then be investigated further via other means.

From these discriminant function analyses, two individuals are consistently given the same species assignment. SK 2366 is consistently predicted to be *A. bondi*, supporting my visual species assignment but surprising, as dietary indicators via use-wear show SK 2366 to be primarily browsing. KA 765 is consistently grouping with *A. recki*. The other specimens show greater variation and either indicate that these measurements, or combination of measurements are not accurate predictor variables for species identification. Or, that the other specimens do not comfortably align with one particular species and are perhaps indeed candidates for *A. australis*. The latter may be particularly relevant to specific cases [SK 3055, SKX 35327, SKX 35320 and SKX 30332], which group with either *A. recki* or fossil or modern *A. marsupialis,* depending on the combination of measurements taken forward. As *A. australis* is potentially a transitional form from the ancestral *A. recki* to the extant *A. marsupialis*, these individuals could represent *A. australis* as a transitional form. This analysis adds a degree of clarity to these unknown specimens by using the 'known individuals' model to make informed predictions for the unknown specimens. However, other factors such as, the degree of sexual dimorphism and overlap between small individuals of one species (*A. marsupialis*) and large individuals from another (*A. recki*) are unknown. Therefore, making any definitive taxonomic classifications unachievable.

Aepyceros? (Impala)

Additional investigation was therefore carried out. One fossil springbok, *A. bondi*, was originally identified as being morphologically similar in dentition to *Aepyceros*. Justifications were made as to why this species aligned more with *Antidorcas* than with *Aepyceros*, despite its many similarities (Vrba 1973). To investigate the *Antidorcas* dentition more fully, this morphologically (dentition) similar species (*Aepyceros*) was used for comparisons with all *Antidorcas* fossil species.

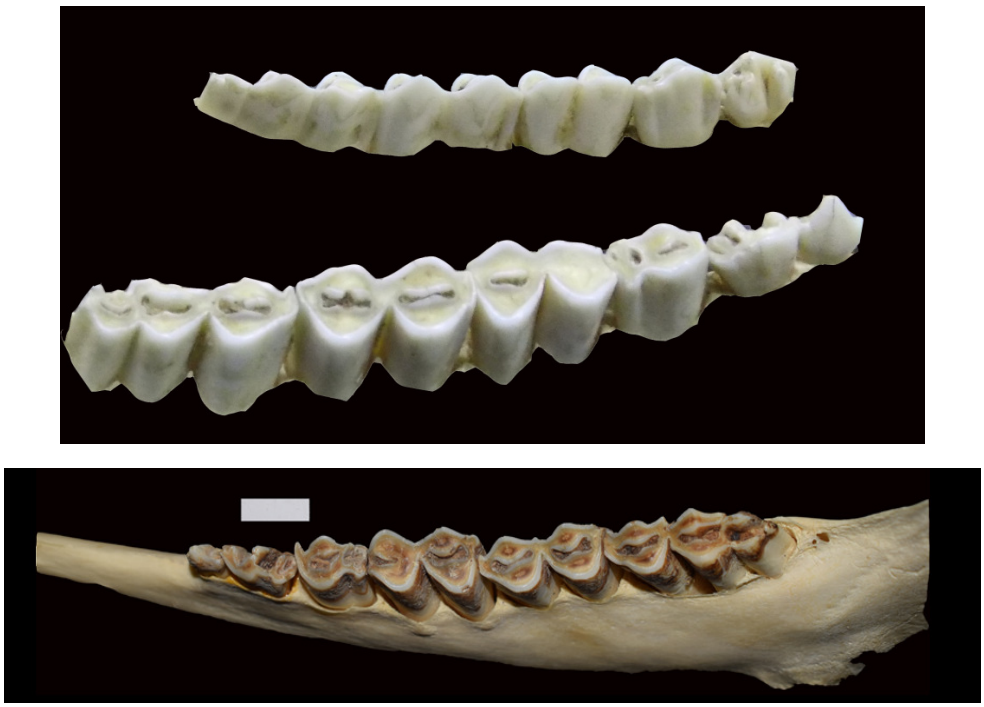


Figure 6.14: Upper image: An example of Aepyceros melampus lower dentition. BP1/C 110 BPI comparative collection, University of the Witwatersrand. Lower image: (original photograph taken by L. Crété) AZ 751 left mandible, Ditsong Museum of Natural History, Pretoria (Mammology department). Scale bar represents 10mm.

Figure 6.15: An example of Aepyceros melampus upper dentition. AZ 532 female impala from Ditsong Museum of Natural History, Pretoria (Mammology department). Original photograph taken by L. Crété.

A collection of modern *Aepyceros melampus* (Figure 6.14-Figure 6.15) upper second molar measurements (measured by Lucile Crété in South Africa in 2017) were added to the dataset of modern and fossil *Antidorcas* upper second molars. A discriminant function analysis was carried out using MDL and BLW as predictor variables. 47% of cases were correctly identified and of those correctly identified, the impala specimens were identified with 71% accuracy.

From this model 7 fossil specimens were predicted as *Aepyceros*, 5 of which were identified previously by other researchers as *A. australis* [SK 3055, SKX 35327, SKX 30334, SKX 35320, SKX 30332], plus SK 3012 (*A. marsupialis*) and KW 8769 (*A. marsupialis*). From visual assessment of these fossil assemblages, there is the possibility of impala being present. However, modern *Antidorcas* and *Aepyceros* also have some inaccuracy in their taxonomic assignments from this model, which appears to be due to an overlap of dental size, based on sexual dimorphism. 31 modern *Aepyceros melampus* specimens were added, of these, 22 are accurately classified as *Aepyceros*. Of the 9 inaccurately classified, 8 are female and 1 is male. 21 modern *Antidorcas marsupialis* specimens are classified as *Aepyceros*. Of these, 5 are female, 11 are male and 4 of unknown sex. *Aepyceros* is larger than *Antidorcas*. Female individuals are typically smaller, thus it is unsurprising that most inaccuracy comes from smaller individuals of the larger species and vice versa.

Given these findings and because the exact degree of sexual dimorphism and the range of inter- and intra-specific size variation of the fossil species is unknown; the chances of accurately differentially identifying *A. australis* from the measurements alone is rendered unfeasible.

6.2.2 Niche Separation and Character Displacement

Diet of *A. australis*

Although not a definitive species identification method, behavioural differences (visible through dietary differences) could hint at potential species differences via ecological separation. These differences can be used in conjunction with morphological information gained here to more holistically inform on taxonomic identifications. The diets of each potential *Antidorcas* specimen will therefore be considered. Diet is inferred from the methods used for this research (mesowear, microwear and isotope analysis). Within each site stratigraphic member, there is the assumption that a temporal overlap between species' populations exists, yet this may not be the case due to time-averaging of deposits. A certain degree of character displacement and niche partitioning would be expected for a separate species living alongside another belonging to the same genus. If the populations of *Antidorcas* are the sole *Antidorcas* species at any one time, competition is likely to be reduced and no niche partitioning is necessary. Differential diets could indicate *potential* species differences, with each species consuming diets representative of their preferred habitat and vegetation. Behavioural changes (visible via dietary indicators) could also be a precursor to evolutionary change (Lister 2013).

If A. australis warrants a separate species classification here, behavioural factors, such as niche partitioning, visible via dietary indicators should be present. If they are present and these individuals also appear morphologically distinct (as indicated in section 6.2.1), an argument can be made in support of identifying *A. australis* as taxonomically distinct from *A. marsupialis*. Each method used to assess dietary behaviour is considered in turn in the following text.

Table 6.23: Antidorcas dietary categories based on each method implemented. Dietary preferences according to microwear, mesowear and carbon isotope indications for each specimen identified as potential Antidorcas australis.

Site and Member	Specimen Number	Mesowear	Microwear	Carbon isotopes $\delta^{13}C$ (‰)	Oxygen isotopes $\delta^{18}O$ (‰)SMOW
Swartkrans Member 1 LB	SKX 5821	[HS (juvenile*)] Browser	x	x	x
	SKX 12067	[HS;HS;H-MS-R] Browser	Mixed	x	x
	SKX 12068	[HS;LS;MS-R] Browser	Mixed	x	x
	SKX 14250	[HS;LR;L-MR-S] Browser-Mixed	Mixed	x	x
	SKX 11602	[HR;LR;MR] Mixed	x	Seasonal mixed	
				-7.45 Mixed	+29.63
				-9.19 Variable Browser	+31.34
				-9.43 Variable Browser	+30.77
				-9.73 Browser	+31.21
				-9.66 Browser	+29.73
				-9.85 Browser	+31.01
	SKX 8455a	[HS;H-MS-R] Browser	x	x	x
	SKX 6331	[LR;LR] Grazer	x	x	x
	SKX 6432	[HR;HR-S] Mixed	x	x	x
	SKX 7066	[HR;LS;MS-R] Mixed	Mixed	x	x
Swartkrans Member 2	SK 1055	[HR;LR;LR-S] Grazer-Mixed	Mixed	-1.6 variable grazer	31.07
	SK 3055	[HS;LR;MR-S] Browser-Mixed	Grazer-Mixed	-11.0 Browser	33.02
	SK 12056	[LR;LR;LR-B] Grazer	x	x	x
	SK 5958	[LR;LR;LR-S] Grazer-Mixed	Mixed	-9.1 variable browser	30.04
	SK 3116	[LR;LR-S] Grazer-Mixed	x	x	x
	SK 2366	[HS;LS;L-MR-S;HS;M-HS-R] Variable Browser	Browser	-5.2 Mixed	+28.59

Site and Member	Specimen Number	Mesowear	Microwear	Carbon isotopes $\delta^{13}C$ (‰)	Oxygen isotopes $\delta^{18}O$ (‰)SMOW
	SK 2115	[LR;MR-S] Mixed	x	x	x
	SK 2953	[LR;LR;LR-B] Grazer	x	-15 Browser	28.70
	SK 14070	[HR;LS;LS-R] Mixed	x	-12.9 Browser	+28.90
	SK 2664	[LB;LB-R] Grazer	x	x	x
Swartkrans Member 3	SKX 32176	[LB;LB;LB-R] Grazer	x	x	x
	SKX 21826+21834+21835	[HR;HR;HR-B] Mixed	x	x	x
	SKX 28008	[HS;HR;MR-S] Variable Browser	x	-9.27 Variable browser	+34.60
				-8.92 Mixed	+37.91
	SKX 29147	[LB] Grazer	x	x	x
	SKX 29278	[LB;LB;LB-R] Grazer	x	x	x
	SKX 46244	[LB;LB] Grazer	x	x	x
	SKX 37809	[HS;HS;HS-R] Browser	x	x	x
	SKX 36347	[HR;LR;LR-S] Mixed	x	x	x
	SKX 32887	[LB;LB-R] Grazer	x	x	x
	SKX 27876	[LR;LB;LB] Grazer	x	x	x
	SKX 27717	[LB;L-MB] Grazer	x	x	x
	SKX 35320	[HR;LS;MR-S] Mixed	Mixed	x	x
	SKX 30334	[HS;HS;H-MS-R] Browser	Mixed	x	x
	SKX 30332	[HS;LR;LR-S] Mixed	x	x	x
	SKX 20143	[HR;HR;MR] Mixed	x	x	x
	SKX 37716	[HR;HR;H-MR-B] Mixed	x	x	x
	SKX 35066	[HS;LS;MS-R] Browser-Mixed	x	x	x
	SKX 35326	[LR;LB;LB] Grazer	x	-10.82 Browser	+31.29

Site and Member	Specimen Number	Mesowear	Microwear	Carbon isotopes $\delta^{13}C$ (‰)	Oxygen isotopes $\delta^{18}O$ (‰)SMOW
	SKX 25562	[HS;MS-R] Browser	x	x	x
	SKX 36545	[LR] Grazer	x	-8.11 Mixed	+29.13
	SKX 35327	[HR;LR;LR-S] Mixed	Mixed	x	x
	SKX 33839	[HS;HS;MS-R] Browser	x	-9.08 Variable browser	+30.83
	SKX 28381	[LR;LR] Grazer	x	x	x
	SKX 35388	[HS;HR;HR-S] Browser-Mixed	x	x	x
	SKX 35384	[LR;HR;HR-B] Mixed	x	x	x
	SKX 37102	[HS;HS;HS] Browser	x	x	x
	SKX 32624	[HS] Browser	x	x	x
	SKX 22287	[LB] Grazer	x	x	x
Swartkrans Member 3	SKX 25040	[HS;HR;HR-S] Browser-Mixed	Mixed	x	x
	SKX 39103	[LR;LR] Grazer	Mixed	x	x
	SKX 39611	[LR;LR] Grazer	x	x	x
	SKX 39719	[HS;LR;L-MR] Mixed	x	x	x
	SKX 28491	[HR;M-HR-B] Grazer-Mixed	x	x	x
	SKX 30875	[LR;LR-B] Grazer	x	x	x
	SKX 29771	[LR;LR-B] Grazer	x	x	x
	SKX 26844	[LB;LB;MB] Grazer	x	x	x
	SKX 28999	[LB] Grazer	x	x	x
	SKX 37821	[LB] Grazer	x	x	x
	SKX 28393	[LR;LS;LS-R] Mixed	x	x	x
	SKX 39908	[LR;LR-S] Mixed	Mixed	x	x
	SKX 38594	[LS;LS-R] Mixed	Mixed	x	x
	SKX 37198	[HS;HS;HS-R] Browser	x	x	x
	SKX 35038	[LR;LR-S] Mixed	x	x	x
	SKX 34250	[LR;LR-B] Grazer	x	x	x

Site and Member	Specimen Number	Mesowear	Microwear	Carbon isotopes $\delta^{13}C$ (‰)	Oxygen isotopes $\delta^{18}O$ (‰)SMOW
	SKX 30878	[HR;LS;L-MS-R] Mixed	x	x	x
	SKX 29420	[LR;LR-S] Mixed	x	x	x
	SKX 30806	[HS;HS;HS]* Browser	x	x	x
	SKX 22254	[LB;LB-R] Grazer	x	x	x
	SKX 27338	[LR;LR;LR-B] Grazer	x	x	x
Swartkrans Member 3	SKX 36803b	[LB;LR;LR-S] Variable grazer	Mixed	x	x
Kromdraai A	KA 901	[LB;LB;LB-R] Grazer	x	x	x
	KA 964b&c	b [LS;LS-R] c [LR;LR-S]	x	x	x
	KA 925	[LR;LR-B] Grazer	Mixed	x	x
	KA 765	[LS;L-MS-R]	Mixed	x	x
	KA 1111	[LS;LS-R] Mixed	Mixed	x	x
	KA 1310	[LR;LB-R] Grazer	x	x	x
	KA 2474	[LS;MS-R] Mixed	x	x	x
	KA 1002	[LR;L-MR-B] Grazer	x	x	x
Sterkfontein Member 4	STS 1325 A	[LR;LR-B] Grazer	x	-13.21^{A}; -13.30^{B} Browser	$+25.80879^{A}$
	STS 2369	[HR;HS-R]	x	-10.46^{A} Browser	$+30.75691^{A}$
	STS 2076	[HS;HS] Browser	Mixed	x	x
	STS 1944	[LS;LS] Mixed	x	-13.97^{A}; -14.00^{B} Browser	$+23.02546^{A}$

Figure 6.16: SK 2366 buccal, occlusal and lingual views. SK2366 displays hyper-hypsodonty infindibular are between U-shaped (as A. recki) and centrally constricted (as A. bondi), pronounced styles without obvious concavity (as present in A. recki), relatively thick enamel, and the squaring of the posterior loph, predominantly characteristic of A. bondi.

The only individual that had distinctive microwear variables indicative of any feeding type, is SK 2366 (Figure 6.16). This individual had a definite browsing signal from all microwear variables and a probable browsing signal from mesowear. This specimen was noted as potentially being *A. bondi* in this study and previous analysis (e.g. Sewell et al. 2019; deRuiter 2003) predominantly because of the extreme hypsodonty displayed. Carbon isotope values show a mix of C_3 and C_4 plants in the diet of SK 2366, i.e. a mixed-feeder.

Mesowear

Mann-Whitney U tests performed on each species group, against the potential *A. australis* specimens, for all mesowear variables on ranked data, showed significant differences. Species were compared in a pairwise fashion with a Bonferroni adjustment, significance level p>0.0125.

Table 6.24: Pairwise comparison of species for mesowear variables, showing where significant differences are found and their significance (p-value).

Pairwise species comparisons	Dentition (upper/lower)	Mesowear variable	Significance

Pairwise species comparisons	Dentition (upper/lower)	Mesowear variable	Significance
recki and potential *australis*	Upper	Relief	0.000
	Lower	x	x
bondi and potential *australis*	Upper	Relief	0.001
		Mesowear III	0.000
	Lower	x	x
Fossil *marsupialis* and potential *australis*	Upper	x	x
	Lower	New mesowear score	0.005
Modern *marsupialis* and potential *australis*	Upper	New mesowear score	0.000
		New relief	0.000
		Mesowear III	0.006
	Lower	New mesowear score	0.002
		New relief	0.000

The same mesowear variables showed significant differences for modern and fossil *marsupialis* for upper dentition (new mesowear score, p=0.001; new relief, p<0.000; Mesowear III p=0.001). See chapter 4 ('mesowear) for a full explanation of these measurements.

As shown in Table 6.24, fossil *marsupialis* and potential *australis* had no significant differences for maxillary dentition. This suggests *A. australis* is not sufficiently different from fossil *marsupialis* to differentiate these two as separate species. No significant differences were found between fossil and modern *marsupialis* for lower dentition either. However, significant differences were found between both fossil *marsupialis* and potential *australis* and modern *marsupialis* and potential *australis*, for the expanded mesowear categories. These new mesowear categories allow a greater degree of variation to be included (see chapter 8). There is the potential that this creates an inflated sense of variation within mixed feeding categories, making a distinction based on minimal differences. Yet the difference could point to species distinction for *A. australis*. It is of note that this falls on the lower dentition, which is often overlooked for mesowear because of its tendency towards blunting of the cusps, thereby giving an overemphasized grazing signal. This result could be an artefact of using lower dentition, or be the result of differential grazing/browsing (or abrasiveness of diet) for *A. marsupialis* and *A. australis*.

Mesowear Discriminant function analysis

In the DFA created to predict species according to mesowear variables (diet), for upper molars (Figure 6.17-Figure 6.18), the predictor model had only 44% accuracy (Table 6.25). However, for lower molars, the predictor model had 91.7% accuracy (Table 6.26).

Table 6.25: Discriminant function analysis results for Antidorcas species upper molar mesowear dietary indicators. A. Summary of canonical discriminant functions: eigenvalues (first 3 canonical discriminant functions were used in the analysis), B. Wilks' Lambda, C. Classification function coefficients, D. Standardised canonical discriminant function coefficients.*

A) Summary of canonical discriminant functions: Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical correlation
1	.485*	73.7	73.7	.571
2	.102*	15.5	89.2	.304

3	.071*	10.8	100.0	.258

B) Wilks' Lambda

Test of Function(s)	**Wilks' Lambda**	**Chi-Square**	**df**	**Significance**
1 through 3	.571	65.663	18	.000
2 through 3	.847	19.406	10	.035
3	.933	8.067	4	.089

C) Classification function coefficients. Fisher's linear discriminant functions.

	Species			
	A. recki	***A. bondi***	**Fossil *A. marsupialis***	**Modern *A. marsupialis***
Mesowear 0-4	-15.224	-15.129	-15.270	-16.173
Relief	96.071	94.693	95.088	99.742
New Mesowear score	4.619	4.489	4.592	4.611
New relief	69.446	66.186	67.974	67.575
New cusp shape	11.031	10.753	10.875	11.824
Mesowear III	-.808	.707	-.248	-2.556
(constant)	-208.925	-200.760	-204.198	-206.777

D) Standardised canonical discriminant function coefficients.

	Function		
	1	**2**	**3**
Mesowear 0-4	-.490	.233	.421
Relief	.856	.207	-.767
New Mesowear score	.696	.903	1.550
New relief	.353	1.660	1.669
New cusp shape	.746	.093	-.591
Mesowear III	-1.147	-.488	.078

Table 6.26: Discriminant function analysis results for Antidorcas species lower molar mesowear dietary indicators. A. Summary of canonical discriminant functions: eigenvalues (first 3 canonical discriminant functions were used in the analysis), B. Wilks' Lambda, C. Classification function coefficients, D. Standardised canonical discriminant function coefficients.*

A) Summary of canonical discriminant functions: Eigenvalues

Function	**Eigenvalue**	**% of Variance**	**Cumulative %**	**Canonical correlation**
1	77.606*	95.7	95.7	.994
2	3.308*	4.1	99.8	.876
3	.156*	.2	100.0	.368

B) Wilks' Lambda

Test of Function(s)	**Wilks' Lambda**	**Chi-Square**	**df**	**Significance**
1 through 3	.003	38.806	15	.001
2 through 3	.201	10.437	8	.236
3	.865	.945	3	.815

C) Classification function coefficients. Fisher's linear discriminant functions.

	Species			
	A. recki	***A. bondi***	**Fossil *A. marsupialis***	**Modern *A. marsupialis***
Mesowear 0-4	481.791	484.814	389.721	481.047
Relief	1640.209	1649.186	1334.279	1648.953
New Mesowear score	195.698	196.953	158.930	195.512
New relief	4424.674	4454.488	3588.233	4414.628
Mesowear III	-63.442	-60.837	-47.256	-66.791
(constant)	-9299.708	-9430.235	-6138.921	-9279.096

D) Standardised canonical discriminant function coefficients.

	Function

	1	2	3
Mesowear 0-4	3.558	.339	-.057
Relief	3.845	-.734	1.406
New Mesowear score	20.339	1.537	.922
New relief	15.378	2.041	-.195
Mesowear III	-.478	.933	.428

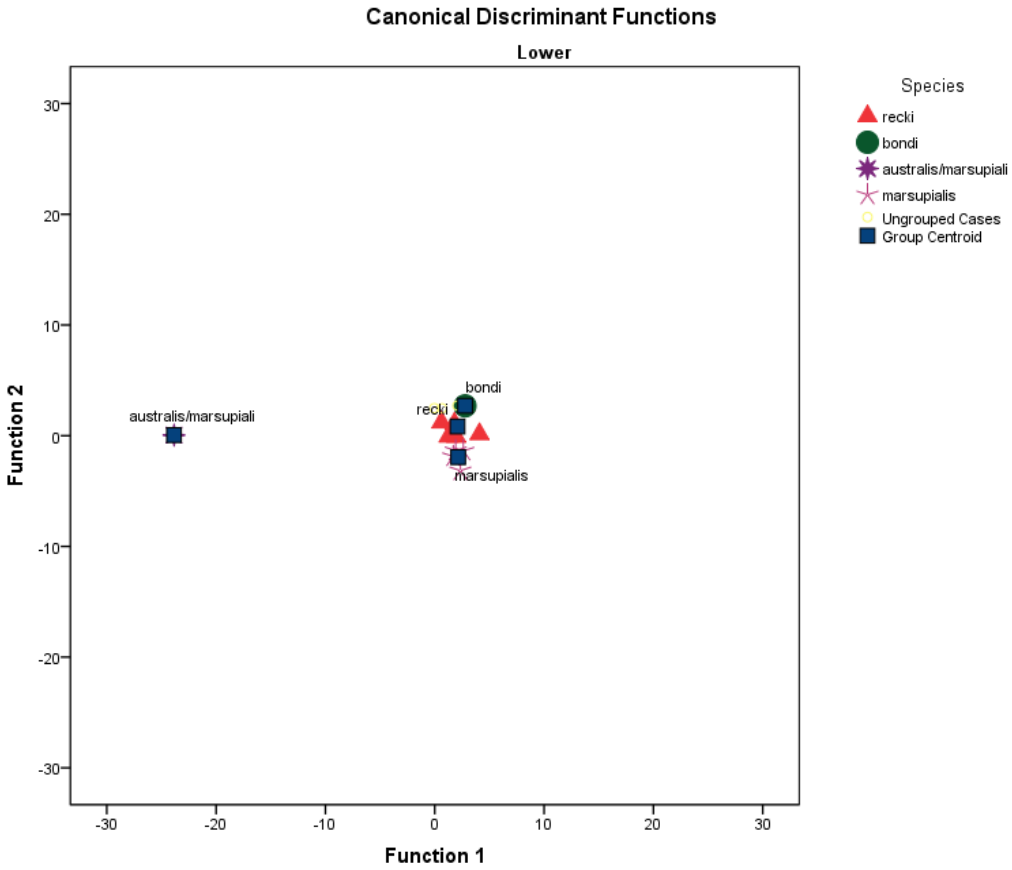


Figure 6.17: Discriminant Function Analysis according to species using all mesowear variables for lower dentition with 91.7% accuracy. 'marsupialis' is modern springbok, 'australis/marsupialis' is fossil A. australis or A. marsupialis (i.e. Antidorcas that is not A. recki or A. bondi). Red triangle shows A. recki, green circle A. bondi, full purple star fossil A. marsupialis, stencil purple star modern A. marsupialis and the group centroid is represented by a blue square. Interestingly, the group that potentially contains A. australis is discriminated separately, indicating a greater degree of variation for this category and possibly showing a mixture of dietary signals from 2 species.

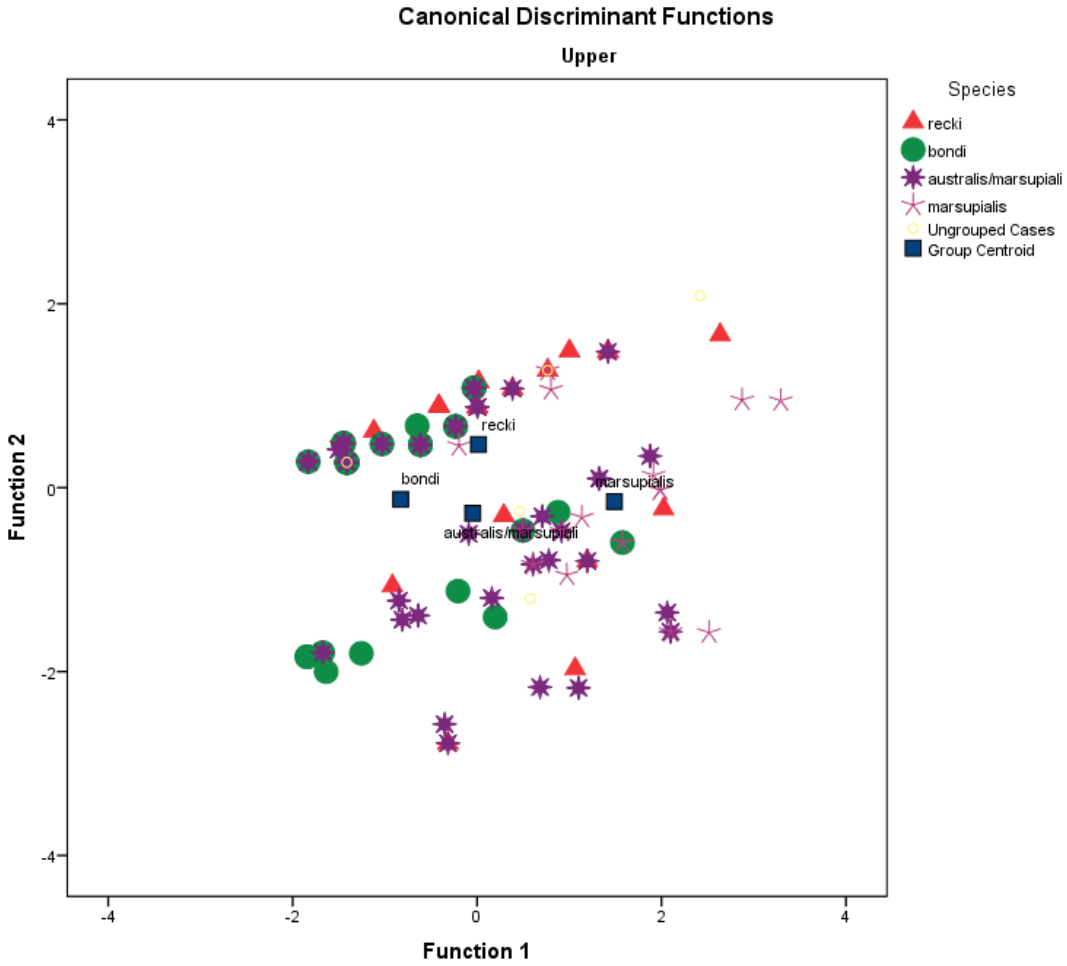


Figure 6.18: DFA for upper dentition according to species with 48% accuracy. Mesowear variables used in the analysis were based on their accuracy as predictor variables. Cusp shape and mesowear scores (1-6) were not used in the analysis as they were not good predictors of species.

DMTA

Potential *A. australis* specimens were considered as individuals (rather than together, taking means as a group representative) when considering the microwear scores, to allow for individual animal preference. Dietary inferences are presented in Table 6.23, DMTA variables are shown here (Table 6.27) to provide more specific detail. Only SK 2366 gave an obvious dietary signal from all microwear variables, of browsing. No niche separation for potential *A. australis* is apparent from these microwear variables (considered in isolation, or when compared to the full dataset; see chapter 9 'DMTA').

Table 6.27: Microwear variables for potential A. australis specimens. Filename shows the specimen number, followed by tooth, side (dex=right, sin=left) and facet (ptc_ml=protocone mesio-lingual facet). Numbers after the filename show if multiple scans were made. 'Molar' denotes where dental facets scanned came from maxillary (upper) or mandibular (lower) dentition. Variables as detailed in chapter 4. The diet column presents the suggested diet based on the previous microwear categories. G=Grazer; MF=Mixed Feeder; B=Browser. Values given to 2 decimal places.

Specimen filename	Molar	Asfc	Smc	StdDev	epLsar ($x10^3$)	HAsfc 9	HAsfc 81	TFV	Diet
SKX12067-UM2-dex-ptc-ml	Upper	2.52	0.07	11.73	4.38	0.21	0.45	46466.08	MF
SKX12068-UM1-dex-ptc-ml	Upper	4.62	0.07	20.85	2.69	0.75	2.18	38816.92	MF
SKX14250-UM2-dex-ptc-ml	Upper	1.40	0.07	11.66	4.28	0.65	0.77	54199.07	MF
SKX7066-lm3-dex-ptcd-db	lower	1.99	0.13	11.86	5.41	1.05	1.49	46129.29	MF
SK3055_UM2_Ptc_ml-1	Upper	20.27	73.52	17.51	6.14	1.06	1.74	57461.24	MF
SK3055_UM2_Ptc_ml-2	Upper	10.12	0.07	12.46	0.93	0.26	0.39	48498.82	G-MF
SK5958.LM2_ptcd_db-1	lower	4.49	0.07	11.92	0.43	0.58	0.75	42455.98	MF
SK2366_UM2_Ptc_ml	Upper	10.91	0.07	16.08	2.53	0.52	0.87	28503.63	B
SK2366_UM2_Ptc_ml-2	Upper	10.37	0.07	16.06	2.58	0.45	0.92	32378.39	B
SK2366_UM2_Ptc_ml-1	Upper	8.86	0.21	34.50	0.42	0.47	0.86	26586.16	B
SK35320_UM2_Ptc_ml-1	Upper	1.51	0.07	11.67	3.61	0.51	0.68	27793.88	MF
SKX30334_UM2_Ptc_ml-1	Upper	12.00	0.07	13.26	7.51	0.54	1.05	31743.41	MF
SK35320_UM2_Ptc_ml-2	Upper	1.42	0.13	11.68	3.67	0.41	0.50	46978.96	MF
SKX30334_UM2_Ptc_ml-1	Upper	12.00	0.07	13.26	7.51	0.54	1.05	31743.41	MF
SKX30334_UM2_Ptc_ml-2	Upper	1.46	0.13	11.71	2.32	0.19	0.40	32352.47	MF
SKX35327_UM2_Ptc_ml-1	Upper	1.18	0.07	11.67	1.85	0.59	0.64	32446.34	MF
SKX25040_UM2_Ptc_ml-1	Upper	2.78	0.07	11.77	2.33	0.41	0.67	46675.23	MF
SK39103-UM2-dex-ptc-ml	Upper	1.16	7.49	11.70	4.22	0.41	0.69	43756.58	MF
SKX39908-lm2-dex-ptcd-db	lower	0.82	0.41	11.66	3.59	0.21	0.48	54705.95	MF
SKX38594-lm3-dex-hypd-db	lower	1.01	13.31	11.69	5.77	1.39	1.38	39198	MF
SKX368036_ptcd_db-1	lower	4.29	0.07	12.28	2.97	0.63	1.07	48553.06	MF
KA925-UM3-dex-ptc-ml	Upper	3.64	0.07	11.89	5.53	0.20	0.63	64082.91	MF
KA765-UM2-sin-ptc-dl	Upper	5.23	0.07	12.05	1.20	0.94	1.34	41754.29	MF
KA111-UM2-sin-ptc-ml	Upper	1.71	26.09	11.81	4.83	0.72	1.70	40833.99	MF
STS2076_LM2_ptcd_db-1	lower	8.93	0.07	13.21	0.15	0.29	0.61	52101.07	MF
STS2076_LM2_ptcd_db-2	lower	12.68	0.13	16.80	2.18	0.52	0.74	47841.7	MF
STS2076.2_LM2_ptcd_db-1	lower	10.23	0.07	29.99	1.65	1.03	1.94	38711.05	MF

6.3 Fossil taxonomic identification and *Antidorcas australis*

CONCLUSIONS

The '*A. australis'* and '*Antidorcas* sp.' dental specimen results outlined in this chapter are considered in isolation and alongside those for all *Antidorcas* species, fossil and modern. Specimens assigned to '*A. australis*' fall within the range of variation for *Antidorcas* (see subsequent methods chapters). From the results presented in this chapter, I conclude that there is insufficient evidence to warrant a distinct *A. australis* species category for the Cradle of Humankind specimens studied here.

Morphologically and behaviourally (via dietary evidence and consequent habitat inferences), *A. australis* does not stand out as a sufficiently distinct grouping. That is not to say that *A. australis* does not exist as a distinct species elsewhere (geographically), or that these specimens could not represent a sub-species of *A. marsupialis,* or a chronospecies, transitionary between *A. recki* and *A. marsupialis*, (as Vrba 1976) but simply that sufficient difference is not found *here* to warrant separation at the species level. Although an assessment of the Cradle of Humankind potential *A. australis* specimens is made, based on the evidence available from this research, the debate regarding the taxonomic identity of *A. australis* in Africa remains unresolved until direct and detailed comparisons are made between at least the Cape and Cradle forms. Only mesowear results indicate the potential separation of *A. australis*, perhaps indicating niche partitioning, via behavioural (dietary) displacement. Unfortunately, the level of time-averaging of the assemblages is unknown within these deposits. The potential exists that the fossil *A. marsupialis* and suggested *A. australis* mesowear differences arise from non-contemporary populations and are not therefore, directly comparative in a mixed feeding lineage. I.e. they could represent two or more *A. marsupialis* populations from different seasons or different years.

Certain specimens were taxonomically re-assigned to *A. recki*, *A. bondi* or *A. marsupialis* from '*A. australis/marsupialis'*. These identifications were supported by evidence evaluated here and will stand for future chapters. These individuals are listed in the appendices data tables (Appendix A10). Based on the evidence presented in this chapter, the '*A. australis*' specimens not alternatively assigned (as above), will henceforth be synonymised with (fossil) '*A. marsupialis'*. Based on morphology, there is overlap between all *Antidorcas* species, as shown in the scatter plots in this chapter. As a genus with mixed-feeding tendencies, it is also unreliable to assign species based on dietary indicators alone. Therefore, those only identifiable to genus level from visual identification, termed '*Antidorcas* sp.' will remain described as such throughout this research. '*Antidorcas* sp.' is included as a category indicative of the genus but with the knowledge that species is uncertain, and results could be skewed for this category as a consequence.

CHAPTER 7

Dental Morphological Measurements

7.1 INTRODUCTION

Dental morphology is a reflection of the longer-term adaptive history of the lineage, as such dental morphology can assist in reflecting dietary behaviour. This chapter explores the dental molar morphology of the *Antidorcas* species and how this morphology may have adapted through time. More specific dietary methods (mesowear, microwear and isotopic analysis) are then applied to the same individuals in subsequent chapters.

Herbivore dental morphology reflects what an animal is capable of eating, via ancestral adaptive forces (and by extension, their ancestral dietary behaviour and habitats) acting upon the dentition during mastication to meet the physical demands of their diet. Adopting a particular diet requires the dentition to be able to withstand forces required to open cellular walls of the plants, in order to benefit from their nutritional contents (Sanson 2006), as well as being able to have the longevity to withstand lifetime dietary pressures, e.g. from an abrasive diet. Due to these extensive masticatory demands, the functional durability of dentition is reflective of the limiting factors impacting upon the animal (Janis & Fortelius 1988). Consequently, herbivore craniodental morphology is a result of evolutionary adaptations to long-term dietary strategies and convergence (e.g. Janis 1988, 1995; Mendoza et al. 2002; Sanson 2006, 2007; Damuth and Janis 2011). For instance, both hypsodonty (tall crown height, usually associated with grazing ungulates as a functional adaptation to withstand a highly abrasive diet) (Janis 1988) and lophodonty (ridging) of molars is related to the fibre-content of the diet (Janis 1988, Sanson et al. 1991). Diet as well as habitat and feeding-style are important factors in determining the level of hypsodonty. The same is likely true for other means of increasing molar durability, such as increased enamel thickness. Selection pressure to evolve more durable dentition is likely to arise from consistently feeding on a diet that is too abrasive for their dental morphology. In addition to dietary adaptations, environmentally-driven exogenous factors can result in dental adaptations. For example, Damuth and Janis (2011) reaffirm the impact of dust and grit as influential factors placing evolutionary demands on the dentition of herbivores. The increased dust/grit content ingested when grazing at a low level in dry environments were shown to be at least as likely to catalyse wear-resistance in teeth, as was the impact of silica (phytoliths) in grasses.

Vrba (1980) suggests that there is a suite of dental characteristics for bovids that should indicate feeding behaviour. However, these include premolar length, buccolingual molar expansion and diastema length. Solounias and Moelleken (1993) and Solounias et al. (1998) for example, show pre-maxillary shape can be used to determine an animals' dietary category (i.e. grazer, browser or mixed feeder). Unfortunately, there are a limited supply of complete cranial remains or toothrows. The majority of dental specimens available for this study come from isolated teeth.

Here, dental measurements are primarily used to identify *Antidorcas* lineage changes and to make inferences regarding the catalysts of dental morphological adaptations. Enamel is less

plastic than bone, requiring substantial selective pressure for adaptation to occur. Population-level and temporary influences would very rarely result in dental morphological change. Therefore, any dental morphological changes apparent can be inferred to be the result of substantial selective pressure and unidirectional change through time are potentially indicative of speciation events.

There are a limited number of ways dentition can adapt to withstand these pressures to enable survival. Adaptations, such as those seen in the extinct springbok, *Antidorcas bondi*, of extreme hypsodonty (see Janis 1998) are believed to be a response to prolonged exposure to a highly abrasive (grazing) diet (Vrba 1970, 1973). Coupled with the extreme hypsodonty feature of tall overall crown height, is the relatively small occlusal dimensions. *A. bondi* is suggested to have the smallest occlusal dimensions when compared to the other *Antidorcas* species (Vrba 1973). Discussion of *A. recki* progressively increasing hypsodonty through time has been addressed by Vrba (1973) with reference to Olduvai specimens and suggestion that overlap in these type of measurements between *Antidorcas* species may become apparent in later deposits. A progression which may reflect increasing grasslands and aridity (Vrba 1970).

Yet Janis (1995) found that mixed-feeders in open habitats were not readily distinguished from catholic grazers; and mixed-feeders in closed habitats were not readily distinguished from faithful browsers. As such, information gained using a primarily mixed-feeding proxy such as *Antidorcas* would benefit from multiple avenues of research to enable more accurate palaeoenvironmental interpretations. Using simple dental metrics in conjunction with palaeodietary indicators (such as the use-wear and isotope methods also implemented in this study) has been proven to be a useful tool for inferring palaeoenvironments (Louys et al. 2015).

7.2 RESULTS

7.2.1 Establishing intra-specific variation and basic descriptive statistics

Siding

No significant differences were found for fossil *Antidorcas* specimens between left- and right- sided dentition of the same tooth position (i.e. left upper second molar showed no significant difference to right upper second molar). Therefore, left and right-sided molars of the same tooth type were combined for analysis.

Sexual dimorphism

Modern *Antidorcas* molar measurements were tested for sexual dimorphism (see chapter 6), as *Antidorcas* are known to display sexual dimorphism in their horncores and to a lesser extent, in their body size (e.g. Reynolds 2005).

Modern *Antidorcas* showed significant differences between males and females for BLW, CH and enamel thickness (points B and D).

Following Cope's rule and Vrba's (1973, 1974) identification of *Antidorcas* dentition, the ancestral *A. recki* displays smaller dentition than descendant *A. marsupialis*. Similar issues (to those for *A. australis/ marsupialis,* see chapter 6) exist therefore, for differentiating

between larger *A. recki* and smaller *A. marsupialis,* to allow delineation of speciation from the ancestral *A. recki* to the descendant *A. marsupialis*.

Although *Antidorcas* species could not be combined here as this would prevent identification of species dental morphology change through time Table 7.2 is included to allow comparison with published sources that may have combined *Antidorcas* by genus/ only been identified to genus level.

Sub-specific differences

No significant differences in linear measurements were found for modern sub-species of *Antidorcas* (data was normally distributed and assed via a one-way ANOVA). This was repeated, separating by sex; again no significant differences were found. Although the postcranial skeleton suggests there may be differences in sub-specific individuals (e.g. Castelló 2016), this is not the case for the dentition (Table 7.1). This supports earlier statements regarding the plasticity of bone over dentition and enables more robust conclusions regarding species evolution (rather than population or sub-species differences) from dentition.

Table 7.1: Descriptive statistics [Mean and range] for modern Antidorcas sub-species occlusal dimensions, separated by tooth type. Only teeth for which there is data are displayed. All values to 2 decimal places.

Sub-species	Tooth	N	Mean MDL	Range MDL	Mean BLW	Range BLW	Mean CH	Range CH
A. marsupialis	UM1	25	13.58	4.80	11.15	2.40	10.08	9.80
	UM2	**31**	**16.09**	**6.30**	**11.61**	**3.90**	**11.71**	**11.30**
	UM3	6	16.98	4.00	9.78	2.40	12.03	4.70
	lm1	16	12.54	3.50	8.11	5.60	9.79	5.40
	lm2	21	14.97	3.90	8.29	5.90	11.21	9.10
	lm3	4	22.65	7.10	7.58	1.80	11.25	6.50
A.m.hofmeyri	UM1	7	14.51	3.70	11.23	2.40	11.91	4.40
	UM2	**8**	**17.35**	**2.10**	**11.84**	**2.20**	**11.63**	**2.60**
	lm1	3	13.43	0.80	7.47	0.20	10.10	0.80
	lm2	3	15.10	0.70	7.50	0.50	10.53	0.10
A.m.angolensis	UM1	5	12.84	1.10	11.42	1.00	6.60	4.40
	UM2	**5**	**16.18**	**0.90**	**11.72**	**1.30**	**7.10**	**10.00**
	UM3	1	17.40	0.00	10.10	0.00	10.50	0.00

7.2.2 Descriptive Statistics for *Antidorcas* UM2 Measurements

Table 7.2: Basics descriptive statistics for the genus Antidorcas (fossil and modern) M^2. All values to 2 decimal places.

	MDL	BLW	CH	OH	TH	EA	EB	EC	ED
N	343	343	242	339	253	227	219	227	207
Mean	**14.82**	**10.47**	**10.10**	**2.51**	**27.35**	**1.07**	**0.81**	**0.71**	**1.55**
Median	14.70	10.5	9.8	2.2	28.5	1.1	0.8	0.7	1.5
Mode	14.7	10.1	9.5	2.2[a]	31.2[a]	1.2	0.8	0.7	1.5
Range	11.3	12.8	20.2	9.5	50.4	1.1	1.0	0.9	2.4
Minimum	8.3	2.2	1.8	0.0	7.3	0.5	0.3	0.4	0.5
Maximum	19.6	15.0	22.0	9.5	57.7	1.6	1.3	1.3	2.9

Antidorcas Lineage

Table 7.3: Number of specimens per species ('N') alongside basic descriptive statistics (mean, mode, median, minimum, maximum and range) for all maxillary second molars (M^2) for Antidorcas specimens measured. All measurements in mm. Mean is given to 2 decimal places, all other values given to 1 decimal place. MDL= Mesio-distal length, BLW= Bucco-lingual width, CH=Crown height, CPH=Cusp height, OH=Overall Height, A-D=Enamel Thickness measurements.

Species		MDL	BLW	CH	OH	TH	A	B	C	D
***Antidorcas* sp.**	**N**	16	16	15	16	14	3	3	3	3
	Mean	**13.88**	**9.81**	**9.63**	**3.15**	**33.15**	**1.17**	**0.63**	**0.67**	**1.37**
	Mode	13.4	8.5	12.1	2.3	35.6	x	0.7	0.7	x
	Median	13.7	9.7	9.6	3.0	32.8	1.2	0.7	0.7	1.6
	Minimum	12.2	7.4	6.5	0.7	20.5	1.0	0.5	0.6	0.7
	Maximum	15.4	12.6	12.7	5.3	57.7	1.3	0.7	0.7	1.8
	Range	3.2	5.2	6.2	4.6	37.2	0.3	0.2	0.1	1.1
***Antidorcas marsupialis* (fossil)**	**N**	28	28	19	36	33	23	23	23	22
	Mean	**15.35**	**11.25**	**11.92**	**2.83**	**23.59**	**1.13**	**0.81**	**0.70**	**1.49**
	Mode	15.4	13.1	x	2.7	31.2	1.2	0.8	0.5	1.5
	Median	15.4	11.3	11.8	2.35	23.2	1.2	0.8	0.7	1.6
	Minimum	10.9	7.6	6.1	0.8	10.9	0.5	0.4	0.4	0.5
	Maximum	18.1	14.7	17.7	6.0	38.4	1.6	1.3	1.1	2.6
	Range	7.2	7.1	11.6	5.2	27.5	1.1	0.9	0.7	2.1
Antidorcas recki	**N**	18	18	8	18	15	19	18	19	14
	Mean	**13.61**	**10.05**	**7.29**	**1.56**	**15.70**	**0.99**	**0.76**	**0.63**	**1.28**
	Mode	13.8	10.1	x	1.7	x	1.1	0.8	0.7	1.5
	Median	13.8	10.1	7.55	1.6	11.0	1.1	0.8	0.6	1.3
	Minimum	10.0	5.7	3.8	1.2	7.3	0.5	0.3	0.4	0.5
	Maximum	16.3	15	9.5	1.7	29.6	1.3	1.3	0.6	1.9
	Range	6.3	9.3	5.7	0.5	22.3	0.8	1.0	0.2	1.4
Antidorcas bondi	**N**	25	25	10	25	23	21	20	21	20
	Mean	**14.65**	**9.52**	**9.34**	**2.16**	**34.81**	**1.07**	**0.89**	**0.81**	**1.72**

	Mode	14.8	9.0	x	1.3	34.3	1.1	0.8	0.7	1.5
	Median	14.7	9.6	8.5	1.9	35.6	1.1	0.9	0.8	1.6
	Minimum	12.6	6.6	7.3	0.0	24.1	0.5	0.4	0.5	1.1
	Maximum	16.6	11.2	13.8	6.1	42.7	1.4	1.3	1.3	2.9
	Range	4.0	4.6	6.5	6.1	18.6	0.9	0.9	0.8	1.8
***Antidorcas marsupialis* (modern)**	**N**	64	64	64	44	x	20	20	20	20
	Mean	**16.0**	**11.4**	**10.8**	**2.9**	x	**1.1**	**0.8**	**0.71**	**1.8**
	Mode	16.4	11.1	11.5	2.7	x	1.0	0.6	0.6	2.1
	Median	16.4	11.6	11.2	2.7	x	1.1	0.7	0.7	1.7
	Minimum	8.3	2.2	1.8	1.4	x	0.9	0.4	0.6	1.2
	Maximum	19.6	14.2	22.0	9.5	x	1.3	1.1	0.9	2.4
	Range	11.3	12.0	20.2	8.1	x	0.4	0.7	0.3	1.2

Table 7.4: Descriptive statistics for Antidorcas second maxillary molars separated by species and provenance (site and member). All measurements in mm. Mean is given to 2 decimal places, all other values given to 1 decimal place. MDL= Mesio-distal length, BLW= Bucco-lingual width, CH=Crown height, OH=Occlusal (cusp) height, TH=Total Height, A-D=Enamel Thickness measurements. Where N=1 for all measurements, 'All' denotes all descriptive statistics and the individual measurement is given. Enamel thickness mean measurements are rounded up to 1 decimal place.

Species	***Provenance***		***MDL***	***BLW***	***CH***	***OH***	***TH***	***A***	***B***	***C***	***D***
Antidorcas* Fossil *marsupialis	Sterkfontein Member 5	**N**	1	1	0	1	1	1	1	1	1
		All	**14.8**	**13.71**	**x**	**1.8**	**12.8**	**1.5**	**0.8**	**1.1**	**1.5**
	Kromdraai (W)	**N**	3	3	0	3	3	3	3	3	3
		Mean	**15.73**	**11.43**	x	**2.37**	**19.07**	**1.3**	**0.7**	**0.6**	**1.3**
		Mode	x	x	x	x	x	x	0.8	0.5	x
		Median	16.4	11.5	x	2.4	18.0	1.4	0.8	0.5	1.7
		Minimum	13.6	10.3	x	1.2	17.2	1.0	0.4	0.5	0.9
		Maximum	17.2	12.5	x	3.5	22.0	1.6	0.8	0.9	1.7
		Range	3.6	2.2	x	2.3	4.8	0.6	0.4	0.4	0.8
	Swartkrans Member 1	**N**	2	2	1	2	2	1	1	1	1

		Mean	**16.3**	**8.95**	**12.1**	**3.45**	**20.05**	**1.0**	**0.7**	**0.5**	**1.0**
		Mode	x	x	12.1	x	x	1.0	0.7	0.5	1.0
		Median	16.3	8.95	12.1	3.45	20.05	1.0	0.7	0.5	1.0
		Minimum	14.5	7.6	12.1	1.5	16.9	1.0	0.7	0.5	1.0
		Maximum	18.1	10.3	12.1	5.4	23.2	1.0	0.7	0.5	1.0
		Range	3.6	2.7	0	3.9	6.3	0	0	0	0
	Swartkrans Member 2	**N**	4	4	4	4	4	3	3	3	3
		Mean	**16.13**	**10.93**	**8.45**	**2.80**	**26.93**	**0.9**	**0.6**	**0.6**	**0.6**
		Mode	x	x	x	x	x	0.8	0.6	x	x
		Median	16.3	10.9	9.1	2.6	29.4	0.8	0.6	0.5	1.8
		Minimum	14.7	10.2	6.1	1.5	20.2	0.8	0.6	0.4	0.8
		Maximum	17.3	11.7	9.5	4.5	31.2	1.2	0.6	0.8	2.1
		Range	2.6	1.5	3.4	3.0	11.0	0.4	0	0.4	1.3
	Swartkrans Member 3	**N**	8	8	8	16	16	8	7	8	8
		Mean	**15.84**	**10.55**	**14.86**	**3.03**	**24.21**	**1.0**	**0.7**	**0.7**	**1.5**
		Mode	x	11.3	x	5.5	x	0.9	0.8	0.7	1.6
		Median	16.2	11.0	15.1	2.7	25.1	1.1	0.8	0.7	1.6
		Minimum	13.2	8.5	11.8	0.8	14.0	0.5	0.4	0.5	0.5
		Maximum	17.9	13.1	17.7	6.0	32.7	1.3	1.1	0.8	2.1
		Range	4.7	4.6	5.9	5.2	18.7	0.8	0.7	0.3	1.6
	Plovers Lake	**N**	4	4	0	4	4	4	4	4	4
		Mean	**13.48**	**12.13**	**x**	**1.43**	**17.55**	**1.2**	**0.8**	**0.9**	**1.5**
		Mode	x	x	x	1.1	x	1.2	x	0.9	x
		Median	13.4	11.7	x	1.2	17.9	1.2	1.2	0.9	1.5
		Minimum	10.9	10.5	x	1.1	10.9	0.9	0.9	0.5	0.5
		Maximum	16.2	14.7	x	2.3	23.6	1.4	1.3	1.0	2.6
		Range	5.3	4.2	x	1.2	12.7	0.5	0.4	0.5	2.1
	Cave of Hearths	**N**	6	7	8	9	3	3	3	3	3

		Mean	**15.02**	**12.1**	**10.27**	**3.43**	**35.5**	**1.3**	**0.9**	**0.7**	**1.7**
		Mode	15.7	x	x	x	x	x	x	x	x
		Median	15.0	12.1	10.4	3.1	38.0	1.2	1.0	0.8	1.7
		Minimum	14.1	11.1	7.8	1.0	30.1	1.1	0.6	0.5	1.5
		Maximum	15.7	13.1	12.4	5.9	38.4	1.5	1.2	0.9	1.8
		Range	1.6	2.0	4	4.9	8.3	0.4	0.6	0.4	0.3
Antidorcas recki	Sterkfontein Member 4	**N**	2	2	1	2	0	2	2	2	1
		Mean	**13.8**	**8.2**	**7.6**	**1.65**	**x**	**0.9**	**0.6**	**0.7**	**1.2**
		Mode	x	x	7.6	x	x	x	x	x	1.2
		Median	13.8	8.2	7.6	1.65	x	0.9	0.6	0.7	1.2
		Minimum	13.7	5.7	7.6	1.0	x	0.8	0.4	0.5	1.2
		Maximum	13.9	10.7	7.6	2.3	x	1.0	0.8	0.8	1.2
		Range	0.2	5.0	0	1.3	0	0.2	0.4	0.3	0
	Kromdraai A	**N**	10	10	6	9	8	10	10	10	9
		Mean	**13.92**	**9.56**	**7.82**	**1.71**	**20.45**	**1.0**	**0.7**	**0.6**	**1.3**
		Mode	13.8	10.1	x	1.2	x	1.0	0.8	0.7	1.6
		Median	13.8	10.0	7.7	1.7	22.1	1.1	0.8	0.6	1.4
		Minimum	10.0	7.5	6.3	1.1	9.7	0.6	0.3	0.4	0.5
		Maximum	16.3	11.0	9.5	2.7	29.6	1.3	1.2	0.7	1.6
		Range	6.3	3.0	3.2	1.6	19.9	0.7	0.9	0.3	1.1
	Kromdraai E	**N**	1	1	0	1	1	1	1	1	0
		All	**14.3**	**8.3**	x	**1.6**	**8.8**	**1.2**	**0.8**	**0.7**	x
	Kromdraai W	**N**	1	1	0	1	1	1	1	1	1
		All	**13.5**	**11.5**	x	**2.1**	**9.3**	**1.1**	**0.9**	**0.7**	**1.1**
	Swartkrans Member 2	**N**	1	1	1	1	1	1	1	1	0
		All	**12.4**	**10.1**	**3.8**	**0.5**	**16.5**	**1.1**	**1.2**	**0.4**	x
	Swartkrans Member 3	**N**	2	2	0	3	3	3	2	3	2
		Mean	**12.11**	**12.0**	x	**1.53**	**9.4**	**0.9**	**0.9**	**0.8**	**1.4**

		Mode	x	x	x	x	x	x	x	x	x
		Median	12.1	12.0	x	1.6	9.9	1.0	0.9	0.7	1.4
		Minimum	10.6	11.6	x	1.3	7.3	0.5	0.4	0.4	0.8
		Maximum	13.6	12.4	x	1.7	11.0	1.2	1.3	1.2	1.9
		Range	3.0	0.8	x	0.4	3.7	0.7	0.9	0.8	1.1
	Plovers Lake	**N**	1	1	0	1	1	1	1	1	1
		All	**13.8**	**15.0**	x	**0.5**	**9.1**	**1.1**	**0.5**	**0.6**	**1.5**
***Antidorcas* sp.**	Sterkfontein Member 5 (W)	**N**	1	1	0	1	0	1	1	1	1
		All	**15.3**	**12.5**	x	**0.7**	x	**1.0**	**0.7**	**0.7**	**1.8**
	Swartkrans Member 2	**N**	15	15	15	15	14	2	2	2	2
		Mean	**13.8**	**9.6**	**9.6**	**3.3**	**33.15**	**1.3**	**0.6**	**0.7**	**1.2**
		Mode	13.4	8.5	12.1	2.3	35.6	x	x	x	x
		Median	13.6	9.7	9.6	3.1	32.8	1.3	0.6	0.7	1.2
		Minimum	12.2	7.4	6.5	1.7	20.5	1.2	0.5	0.6	0.7
		Maximum	15.4	12.6	12.7	5.3	57.7	1.3	0.7	0.7	1.6
		Range	3.2	5.2	6.2	3.6	37.2	0.1	0.2	0.1	0.9
Antidorcas bondi	Sterkfontein Member 5	**N**	7	7	2	7	6	7	7	7	6
		Mean	**14.46**	**9.29**	**8.6**	**1.76**	**36.03**	**1.2**	**0.9**	**0.9**	**1.7**
		Mode	x	10.5	x	1.8	34.3	1.1	0.8	0.9	1.5
		Median	14.5	9.6	8.6	1.8	35.2	1.2	0.9	0.9	1.6
		Minimum	12.6	6.6	7.4	1.0	31.1	1.0	0.7	0.7	1.2
		Maximum	16.6	10.5	9.8	2.2	42.7	1.4	1.2	1.0	2.3
		Range	4.0	3.9	2.4	1.2	11.6	0.4	0.5	0.3	1.1
	Sterkfontein unstratified	**N**	1	1	1	1	1	1	1	1	1
		All	**13.7**	**11.2**	**9.3**	**0.0**	**37.3**	**1.2**	**1.1**	**1.3**	**2.4**
	Kromdraai A	**N**	2	2	1	2	2	2	2	2	2
		Mean	**15.3**	**10.25**	**8.1**	**1.3**	**33.2**	**1.4**	**0.8**	**0.7**	**1.7**

	Mode	x	x	8.1	x	x	x	x	0.7	x
	Median	15.3	10.3	8.1	1.4	36.2	1.1	0.8	0.7	1.6
	Minimum	14.8	10.1	8.1	1.3	33.2	0.8	0.7	0.7	1.5
	Maximum	15.8	10.4	8.1	1.5	39.1	1.4	0.8	0.7	1.7
	Range	1.0	0.3	0	0.2	5.9	0.6	0.1	0	0.2
Swartkrans Member 2	**N**	5	5	1	5	5	4	4	4	4
	Mean	**14.56**	**9.28**	**13.80**	**1.92**	**34.98**	**0.8**	**0.7**	**0.6**	**1.6**
	Mode	14.7	x	13.8	1.3	x	x	x	0.5	x
	Median	14.7	9.1	13.8	2.2	35.7	0.8	0.7	0.6	1.6
	Minimum	13.9	8.2	13.8	1.3	28.9	0.5	0.4	0.5	1.3
	Maximum	15.1	10.2	13.8	2.5	40.0	1.1	1.0	0.8	1.9
	Range	1.2	2.0	0	1.2	11.1	0.6	0.6	0.3	0.6
Swartkrans Member 3	**N**	1	1	0	1	1	1	0	1	1
	All	**16**	**8.9**	x	**3.2**	**24.1**	**0.9**	x	**0.9**	**1.5**
Plovers Lake	**N**	5	5	1	5	5	5	5	5	5
	Mean	**14.18**	**9.92**	**8.0**	**1.82**	**31.7**	**1.2**	**1.0**	**0.9**	**1.9**
	Mode	x	x	8	1.9	x	x	0.9	0.7	x
	Median	14.3	9.8	8	1.9	31.5	1.2	1.0	0.8	1.6
	Minimum	13.4	9.2	8	1.3	29.5	0.9	0.9	0.7	1.4
	Maximum	15.2	10.9	8	2.5	35.6	1.4	1.3	1.2	2.9
	Range	1.8	1.7	0	1.2	6.1	0.5	0.4	0.5	1.5
Cave of Hearths	**N**	4	4	4	4	3	1	1	1	1
	Mean	**15.25**	**9.08**	**9.25**	**4.23**	**39.13**	**0.7**	**0.8**	**0.6**	**1.1**
	Mode	x	x	x	x	x	0.7	0.8	0.6	1.1
	Median	15.3	8.9	8.5	4.3	39.9	0.7	0.8	0.6	1.1
	Minimum	14.7	7.8	7.3	2.3	36.5	0.7	0.8	0.6	1.1

	Maximum	15.8	10.7	12.7	6.1	41.0	0.7	0.8	0.6	1.1
	Range	1.1	2.9	5.4	3.8	4.5	0	0	0	0

7.2.3 ENAMEL THICKNESS across the toothrow

Enamel thickness variation across the toothrow (M^2 is excluded as it is evaluated above alongside other dental measurements) for each species is given in the tables (Table 7.5, Table 7.6) below. Enamel thickness is rarely considered in studies of bovid palaeodiets but is a key indicator of dietary abrasiveness.

Table 7.5: Descriptive statistics for Antidorcas enamel thickness according to species for maxillary molars. All measurements are in millimetres (mm). Standard deviation and median values are given to 2 decimal places.

Upper M1								
Species	**N**	**Measurement location**	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**	**Range**	**Median**
A. recki	13	A	1.18	0.18	0.9	1.4	0.5	1.20
		B	0.85	0.21	0.5	1.2	0.7	0.80
		C	0.76	0.16	0.5	1.0	0.5	0.70
		D	1.29	0.34	0.8	1.9	1.1	1.20
A. bondi	4	A	1.13	0.28	0.8	1.4	0.6	1.15
		B	1.10	0.29	0.8	1.5	0.7	1.05
		C	0.83	0.10	0.7	0.9	0.2	0.85
		D	1.68	0.56	1.0	2.3	1.3	1.70
Fossil *A. marsupialis*	10	A	1.20	0.18	0.8	1.5	0.7	1.20
		B	0.81	0.22	0.5	1.2	0.7	0.80
		C	0.71	0.17	0.5	1.0	0.5	0.70
		D	1.11	0.34	0.9	2.0	1.1	1.30
Upper M3								
Species	**N**	**Measurement location**	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**	**Range**	**Median**
A. recki	6	A	0.933	0.47	0.0	1.3	1.3	1.10

Upper M1								
Species	**N**	**Measurement location**	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**	**Range**	**Median**
		B	0.750	0.28	0.3	1.1	0.8	0.80
		C	0.700	0.23	0.4	1.0	0.6	0.70
		D	1.267	0.20	1.1	1.6	0.5	1.20
A. bondi	9	A	1.133	0.44	0.0	1.4	1.4	1.30
		B	1.067	0.19	0.7	1.3	0.6	1.10
		C	0.900	0.13	0.7	1.1	0.4	0.90
		D	1.578	0.25	1.2	2.0	0.8	1.60
Fossil *A. marsupialis*	7	A	1.014	0.18	0.8	1.3	0.5	1.00
		B	0.771	0.16	0.6	1.1	0.5	0.70
		C	0.700	0.14	0.7	1.1	0.4	0.70
		D	1.086	0.23	0.9	1.4	0.5	0.90

Table 7.6: Descriptive statistics for Antidorcas enamel thickness according to species for mandibular dentition. All measurements are in millimetres (mm). Mean, standard deviation and median values are given to 2 decimal places.

Lower M1								
Species	**N**	**Measurement location**	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**	**Range**	**Median**
A. recki	5	A	0.96	0.21	0.70	1.20	0.5	1.00
		B	0.62	0.18	0.40	0.80	0.4	0.60
		C	0.66	0.11	0.50	0.80	0.3	0.70
A. bondi	3	A	0.97	0.15	0.80	1.10	0.3	1.00
		B	0.60	0.30	0.30	0.90	0.6	0.60
		C	1.10	0.00	1.10	1.10	0.0	1.10
Fossil *A. marsupialis*	7	A	1.07	0.46	0.70	1.60	0.9	1.00
	2	B	0.55	0.00	0.20	0.90	0.7	0.55
	5	C	0.82	0.14	0.50	1.10	x	0.90

Lower M1								
Species	**N**	**Measurement location**	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**	**Range**	**Median**
Lower M2								
Species	**N**	**Measurement location**	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**	**Range**	**Median**
A. recki	10	A	0.99	0.25	0.60	1.50	0.9	1.00
		B	0.34	0.22	0.10	0.70	0.6	0.30
		C	0.70	0.16	0.50	1.0	0.5	0.70
A. bondi	18	A	1.13	0.23	0.60	1.50	0.9	1.10
		B	0.58	0.29	0.10	1.10	1.0	0.65
		C	0.76	0.22	0.30	1.10	0.8	0.75
Fossil *A. marsupialis*	10	A	1.20	0.12	1.00	1.40	0.4	1.20
		B	0.45	0.20	0.10	0.70	0.6	0.50
		C	0.74	0.23	0.30	1.10	0.80	0.75
Lower M3								
Species	**N**	**Measurement location**	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**	**Range**	**Median**
A. recki	10	A	1.05	0.14	0.80	1.20	0.4	1.05
		B	0.49	0.20	0.20	0.80	0.6	0.50
		C	0.64	0.15	0.40	0.90	0.5	0.65
A. bondi	5	A	1.34	0.15	1.20	1.50	0.3	1.30
		B	0.78	0.22	0.50	1.10	0.6	0.80
		C	0.82	0.47	0.00	1.20	1.2	1.00
Fossil *A. marsupialis*	3	A	1.00	0.10	0.90	1.10	0.2	1.00
		B	0.70	0.20	0.50	0.90	0.4	0.70
		C	0.70	0.10	0.60	0.80	0.2	0.70

7.2.4 Further statistical analysis for *Antidorcas* measurements

Maxillary Second Molar (UM2)

Provenance Significant differences

- *A. bondi* occlusal (cusp) height across provenance (p=0.031 Independent samples Kruskal Wallis Test).

Table 7.7: Antidorcas bondi significant differences in upper second molar measurements through time. 'N' = number of specimens, 'P' = p-value. The top row states the measurement that shows significant difference through time. The underlined value shows the larger measurement.

Species	Member	N	Mean	*P*
A. bondi	Occlusal (cusp) height across provenance			0.031
A. bondi	Sterkfontein Member 5	7	1.76 mm	0.011
	Swartkrans Member 3	1	3.22 mm	
	Swartkrans Member 2	5	1.92 mm	0.019
	Cave of Hearths	4	4.23 mm	
	Plovers Lake	5	1.82 mm	0.014
	Cave of Hearths	4	4.23 mm	

- Fossil *A. marsupialis* crown height (p=0.003 Independent samples Kruskal Wallis Test).

Table 7.8: Antidorcas marsupialis significant differences in upper second molar measurements through time. 'N' = number of specimens, 'P' = p-value. The top row states the measurement that shows significant difference through time. The underlined value shows the larger measurement.

Species	Member	N	Mean	*P*
A. marsupialis	Crown height across provenance			0.003
A. marsupialis	Swartkrans Member 2	4	8.45 mm	0.001
	Swartkrans Member 3	8	14.86 mm	
	Swartkrans Member 3	8	14.86 mm	0.000
	Cave of Hearths	6	10.27 mm	

Species significant differences

All measurements were significantly different across species p<.000 when analysed by an independent-samples kruskal-Wallis test for all measurements (MDL, BLW, OH, CH, TH). Post-hoc Mann-Whitney U pairwise tests with Bonferroni adjusted significance-levels revealed where these differences were found and are detailed below (Table 7.9).

Interestingly, enamel thickness significantly differed between tooth position only at point B (central enamel band) (see Figure 4.15) for all *Antidorcas* species, including modern springbok. *A. recki* also showed a significant difference (Independent samples Mann Whitney U Test) of enamel thickness at point B between left and right sided upper second molars (p=0.008).

Table 7.9: Post-hoc Pairwise comparisons of dental morphological measurements for each Antidorcas species. Significant differences are indicated by their abbreviation.

	A.bondi	A.recki	A.aus/mars.	modern
A.bondi		MDL,CH,TH,EC,ED	BLW,CH,TH	MDL,BLW,OH,EC
A.recki			MDL,BLW,H,OH,TH	MDL,BLW,CH,TH,ED
A.aus/mars				ED
modern				

Table 7.10: Significant dental size differences between Antidorcas bondi and recki. P=p-value. 'Direction' simply denotes which species yielded the larger/smaller measurement.

Measurement	Species	Mean (in mm)	*P*	Direction
MDL	*A. bondi*	14.65	0.009	longer
	A. recki	13.61		shorter
CH	*A. bondi*	9.34	0.046	higher
	A. recki	7.29		lower
TH	*A. bondi*	34.81	<0.000	higher
	A. recki	15.70		lower
EC	*A. bondi*	0.81	0.005	thicker
	A. recki	0.63		thinner
ED	*A. bondi*	1.72	0.005	thicker
	A. recki	1.28		thinner

Table 7.11: Significant dental size differences between Antidorcas recki and marsupialis. P=p-value. 'Direction' simply denotes which species yielded the larger/smaller measurement.

Measurement	Species	Mean (in mm)	*P*	Direction
MDL	*A. recki*	13.61	0.001	shorter
	A. marsupialis	15.35		longer
BLW	*A. recki*	10.05	0.043	shorter
	A. marsupialis	11.25		longer
CH	*A. recki*	7.29	<0.000	lower
	A. marsupialis	11.93		higher
OH	*A. recki*	1.56	<0.000	lower
	A. marsupialis	2.83		higher
TH	*A. recki*	15.70	0.001	lower
	A. marsupialis	23.59		higher

As shown in Table 7.11, *A. recki* had significantly smaller dentition than fossil *A. marsupialis,* supporting previous studies (e.g. Vrba 1970; Gentry 1978; Reynolds 2005).

Table 7.12: Significant dental size differences between Antidorcas bondi and marsupialis. P=p-value. 'Direction' simply denotes which species yielded the larger/smaller measurement.

Measurement	Species	Mean (in mm)	*P*	Direction
BLW	*A. bondi*	9.52	<0.000	shorter
	A. marsupialis	11.25		longer
CH	*A. bondi*	9.34	0.028	lower
	A. marsupialis	11.92		higher
TH	*A. bondi*	34.81	<0.000	higher
	A. marsupialis	23.59		lower

Table 7.13: Significant dental size differences between fossil Antidorcas species and modern springbok. P=p-value. 'Direction' simply denotes which species yielded the larger/smaller measurement.

Measurement	Species	Mean (in mm)	*P*	Direction
MDL	*A. bondi*	14.65	0.001	shorter
	Modern *A. marsupialis*	16.00		longer
	A. recki	13.61	<0.000	shorter
	Modern *A. marsupialis*	16.00		longer
BLW	*A. bondi*	9.52	<0.000	shorter
	Modern *A. marsupialis*	11.4		longer
	A. recki	10.05	0.011	shorter
	Modern *A. marsupialis*	11.4		longer

Measurement	Species	Mean (in mm)	*P*	Direction
OH	*A. bondi*	2.16	0.046	lower
	Modern *A. marsupialis*	2.90		higher
	A. recki	1.56	<0.000	lower
	Modern *A. marsupialis*	2.90		higher
CH	*A. recki*	7.29	0.001	lower
	Modern *A. marsupialis*	10.80		higher
EC	*A. bondi*	0.81	0.037	thicker
	Modern *A. marsupialis*	0.71		thinner
ED	*A. recki*	1.28	<0.000	thinner
	Modern *A. marsupialis*	1.80		thicker
	Fossil *A. marsupialis*	1.49	0.043	thinner
	Modern *A. marsupialis*	1.80		thicker

UM2 has been used as the primary molar across all methods in this research. However, to more definitively assess species differences and species adaptations through time, the other molar teeth (upper 1st and 3rd molars and lower 1st, 2nd and 3rd molars) were statistically analysed. Basic descriptive statistics are included in Appendices (Appendix A6).

The following results include all molars, as identified in each reporting of results.

Significant Difference Through Time (all tooth types)

Antidorcas recki

Table 7.14: Antidorcas recki significant differences in mandibular dental measurements through time. 'N'=number of specimens, 'P'=p-value / significance. 'Direction' simply denotes which species yielded the larger/smaller measurement.

Measurement	Provenance	N	Mean (in mm)	*P*	Direction
OH across mandibular toothrow	Cooper's Cave	7	3.54	<0.000	higher
	Sterkfontein Member 5	14	1.81		lower
	Cooper's Cave	7	3.54	<0.000	higher
	Kromdraai A	7	1.69		lower
	Cooper's Cave	7	3.54	0.001	higher
	Swartkrans Member 3	11	1.63		lower
TH across the mandibular toothrow	Cooper's Cave	7	26.94	0.001	higher
	Swartkrans Member 3	11	10.82		lower

Maxillary dentition TH showed significant differences for Swartkrans Member 3 (n=12, mean=10.93mm), being smaller than those from Kromdraai A (n=12, mean=21.81mm). The lower second molar (lm_2) of *A. recki* displayed significant differences through time for mesio-distal length (p=.044), occlusal height (p=.024) and total height (p=.013). Post-hoc Mann Whitney U with Bonferroni adjusted alpha levels (significance above 0.003) showed these differences to be between Kromdraai W and Cooper's Cave (p=.001) for MDL; Kromdraai A and Cooper's Cave (p=.001) for OH and (p=.002) for TH. Cooper's Cave A. recki displayed larger MDL, OH and TH than either Kromdraai *A. recki* assemblage.

Table 7.15: A. recki LM_2 mean and standard error of the mean (SEM) for each statistically significant measurement. Only provenance with A. recki LM_2 included. All measurements given in millimetres to 2 decimal places.

Provenance	N MDL	Mean MDL	OH SEM	N OH	Mean OH	OH SEM	N TH	Mean TH	TH SEM
Sterkfontein Member 4	3	13.67	0.94	3	2.30	0.42	3	18.27	2.43
Swartkrans Member 1 LB	2	11.50	0.60	2	1.65	0.03	1	6.50	X
Swartkrans Member 2	2	12.45	0.25	2	1.80	0.30	2	22.50	3.80
Kromdraai A	6	13.12	0.43	6	1.73	0.23	6	20.00	2.85
Kromdraai W	2	11.30	0.30	2	0.80	0.80	2	6.90	0.70
Plovers Lake	1	12.60	X	1	2.00	X	1	11.50	X
Cooper's Cave	6	13.38	0.19	6	3.52	0.19	6	27.88	0.94

Table 7.15 highlights that Kromdraai W shows consistently smaller dentition for these measurements, most similar to those from Swartkrans Member 1 LB. In contrast, Cooper's cave shows consistently larger dentition.

A. bondi Maxillary dentition occlusal height differed significantly from the smaller Sterkfontein Member 5 specimens (n=14, mean=1.64mm) compared to the later Cave of Hearths *A. bondi* (n=4, mean=4.23mm). All other measurements showed no significant change.

A. marsupialis (fossil)

The bucco-lingual width (BLW) of lower first molars (lm_1) varied significantly through time (p=0.036). *A. marsupialis* lm_1 BLW increased from Swartkrans Member 1 to Swartkrans Member 3 (Table 7.17)

Additional significant differences were found for maxillary dentition crown height, bucco-lingual width and total height. Swartkrans Member 3 *A. marsupialis* (n=26, mean=13.67mm) had significantly higher crowned maxillary dentition than was evident in the earlier deposits of Swartkrans Member 2 (n=6, mean=9.43mm) (p=.001) yet were significantly shorter in total height (SKX M3 mean=26.20mm) and narrower bucco-lingually (mean=9.77mm) (p=.001), for Swartkrans Member 3 than was evident at the Cave of Hearths (n=5, mean BLW=11.30mm, mean TH=36.60mm) (TH p=<.000).

Table 7.16: Fossil A. marsupialis total heights (TH) for lower dentition. Only provenance deposits with A. marsupialis present are shown. All measurements in mm and shown to 2decimal places.

Provenance	N	Mean TH	TH SEM
Sterkfontein Member 5	1	12.80	X
Swartkrans Member 1	8	25.03	1.74
Swartkrans Member 1 LB	3	32.53	2.64
Swartkrans Member 2	27	22.18	1.04
Swartkrans Member 3	4	29.06	1.71
Plovers Lake	2	22.40	4.50

Cave of Hearths	2	12.65	4.85

Table 7.16 shows a large jump in total height from smaller dentition ~1.8/1.7 Ma (Sterkfontein Member 5 and Plovers Lake) to more than double by the later dates evidenced by the Cave of Hearth samples ~0.8 Ma. However, earlier deposits have extremely small sample sizes (n=1 or 2), making any conclusions based on this jump tentative at best.

Table 7.17: Mean bucco-lingual width (BLW) measurements for fossil A. marsupialis LM_1. Only provenance with A. marsupialis lm_1 present are shown. All measurements in mm and shown to 2 decimal places.

Provenance	N	Mean BLW	BLW SEM
Sterkfontein Member 5	2	7.60	0.40
Swartkrans Member 1	3	6.13	0.33
Swartkrans Member 1 LB	1	6.80	X
Swartkrans Member 3	8	7.36	0.11

Lower third molars show more variation across species mesio-distally than bucco-lingually (Appendix A6).

Species Significant Differences

Table 7.18: Significant differences between species for molars other than M1s and M3s. The top row states the overall significance across species, with the detail regarding where the differences lie, and their individual significance in the rows below. 'N'=number of specimens, 'P'=p-value / significance. 'Direction' simply denotes which species yielded the larger/smaller measurement.

Tooth type	Measurement	Species	N	Mean (in mm)	*P*	Direction
UM1	MDL	Across species			*p*=0.049	
		A. recki	5	13.62	0.008	shorter
		Modern *A. marsupialis*	37	13.66		longer
	TH	Across species			*p* <0.000	
		A. recki	21	13.89	<0.000	Lower
		Fossil *A. marsupialis*	27	23.04		Higher
		A. recki	21	13.89	0.001	Lower
		A. bondi	4	32.08		higher
	OH	Across species			*p*=0.010	
		A. recki	5	3.50	0.004	Higher
		Fossil *A. marsupialis*	20	3.17		lower
UM3	MDL	Across species			*p*=0.001	
		A. bondi	6	14.37	0.018	shorter
		Fossil *A. marsupialis*	9	16.10		longer
		A. bondi	6	14.37	0.012	shorter
		Modern *A. marsupialis*	7	17.04		longer
		A. recki	8	14.38	0.045	shorter
		Modern *A. marsupialis*	7	17.04		longer
	TH	Across species			*p* <0.000	
		A. recki	8	20.55	<0.000	lower
		A. bondi	12	37.11		higher
	OH	*A. recki*	8	1.39	0.004	lower
		Fossil *A. marsupialis*	9	3.18		higher

Tooth type	Measurement	Species	N	Mean (in mm)	*P*	Direction
		A. recki	8	1.39	0.001	lower
		Modern *A. marsupialis*	7	3.60		higher
lm1	MDL	Across species			*p*=0.002	
		A. bondi	6	11.12	0.047	shorter
		Modern *A. marsupialis*	19	12.68		longer
		A. recki	8	11.48	0.010	shorter
		Modern *A. marsupialis*	19	12.68		longer
	BLW	Across species			*p*=0.004	
		A. bondi	6	6.12	0.001	Shorter
		Modern *A. marsupialis*	19	8.01		longer
	TH	Across species			*p* <0.000	
		A. recki	15	11.42	0.007	lower
		Fossil *A. marsupialis*	15	21.89		higher
	CH	Across species			*p*=0.005	
		A. recki	8	7.30	0.050	lower
		Fossil *A. marsupialis*	10	11.52		higher
lm2	MDL	Across species			*p* <0.000	
		A. recki	22	13.02	0.035	shorter
		Fossil *A. marsupialis*	11	13.97		longer
		A. recki	22	13.02	<0.000	shorter
		Modern *A. marsupialis*	24	14.99		longer
		A. bondi	31	13.34	<0.000	shorter
		Modern *A. marsupialis*	24	14.99		longer
	BLW	Across species			*p* <0.000	
		A. bondi	31	6.52	<0.000	shorter
		Fossil *A. marsupialis*	11	8.21		longer
		A. bondi	31	6.52	<0.000	shorter
		Modern *A. marsupialis*	24	8.19		longer
		A. recki	22	6.39	0.002	shorter
		Fossil *A. marsupialis*	11	8.21		longer
		A. recki	22	6.39	<0.000	shorter
		Modern *A. marsupialis*	24	8.19		longer
	TH	Across species			*p* <0.000	
		A. recki	25	19.03	<0.000	lower
		A. bondi	28	32.51		higher
		A. bondi	28	32.51	0.003	higher
		Fossil *A. marsupialis*	21	22.17		lower
	CH	Across species			*p* <0.000	
		A. recki	22	8.34	<0.000	lower
		Modern *A. marsupialis*	24	11.13		higher
		A. bondi	31	8.93	<0.000	lower
		Modern *A. marsupialis*	24	11.13		higher
lm3	MDL	Across species			*p*=0.002	

Tooth type	Measurement	Species	N	Mean (in mm)	*P*	Direction
		A. bondi	16	20.04	0.050	shorter
		Modern *A. marsupialis*	4	22.65		longer
		A. recki	9	19.14	0.001	shorter
		Modern *A. marsupialis*	4	22.65		longer
	TH	Across species			*p* <0.000	
		A. recki	14	20.21	0.022	lower
		Fossil *A. marsupialis*	10	28.55		higher
		A. recki	14	20.21	0.001	lower
		A. bondi	22	31.18		higher
	OH	Across species			*p*=0.001	
		A. bondi	16	1.63	0.016	lower
		Modern *A. marsupialis*	4	4.43		higher
		A. recki	9	1.72	0.008	lower
		Modern *A. marsupialis*	4	4.43		higher

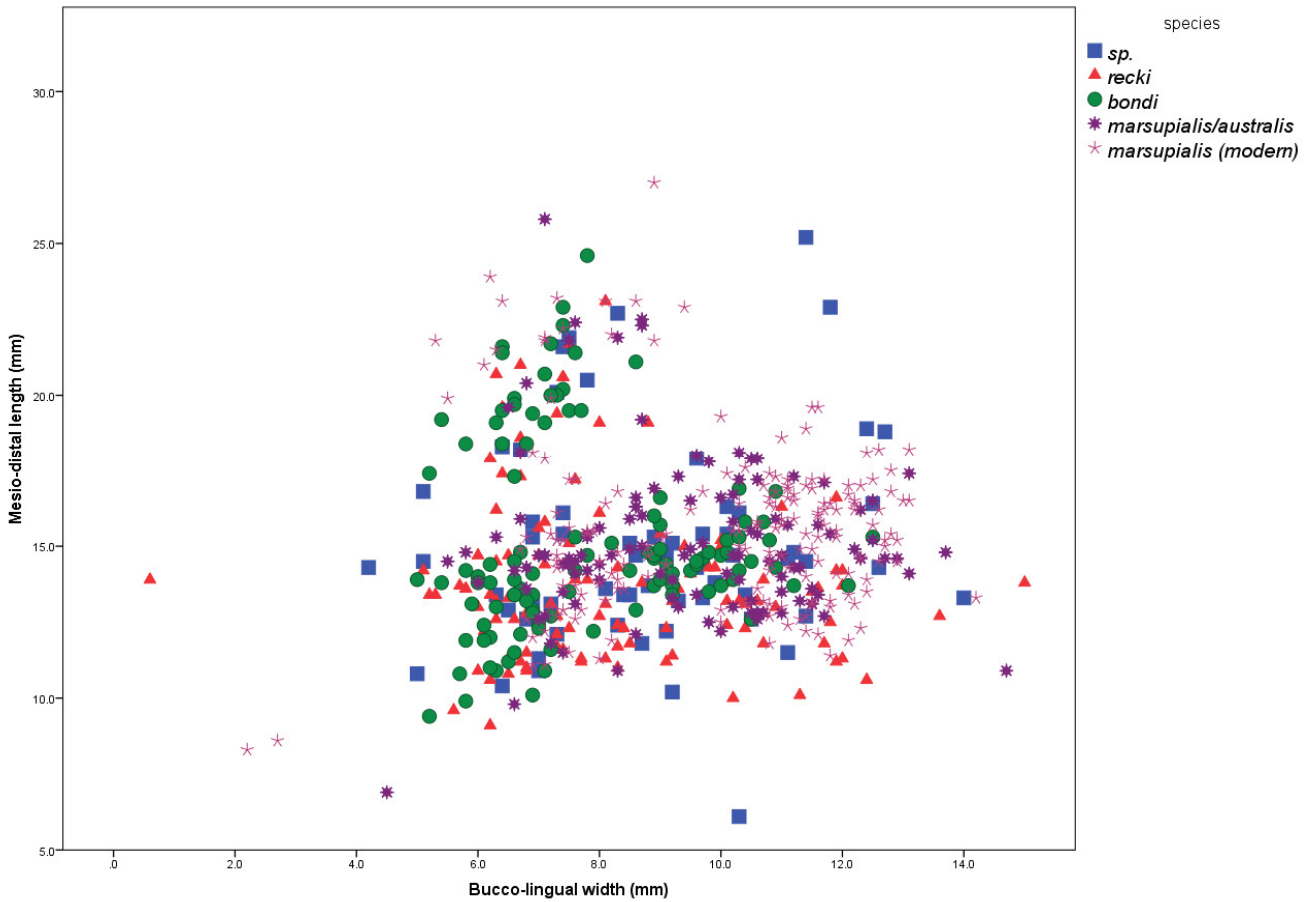


Figure 7.1: Scatter plot comparing dental morphology area (BLW x MDL) of all Antidorcas species UM2 dentition. All measurements in mm. Two clusters appear to form for all Antidorcas species. Most individuals from all species fall within the range of variation for modern species.

The two distinct groupings identifiable in Figure 7.1 could be indicative of sexual dimorphism for all *Antidorcas* species. Modern and fossil *Antidorcas* display sexual dimorphism in their horncores (see Appendix A4), and may be expected to show likewise, albeit to a lesser extent, in their dentition. Unfortunately, a greater number of methods, incorporating more dental landmarks would be required to say this conclusively.

Moreover, these plots (Figure 7.2, and to a lesser extent, Figure 7.8) represent time-averaged species dental morphologies, as such, these apparent groupings could also be indicative of adapting populations of *Antidorcas* incorporated through time within the collection of deposits.

When considering each Member individually (Figure 7.2), sexual dimorphism or species niche partitioning typically becomes more prevalent as sample size increases. These groupings are not due to species differentiations.

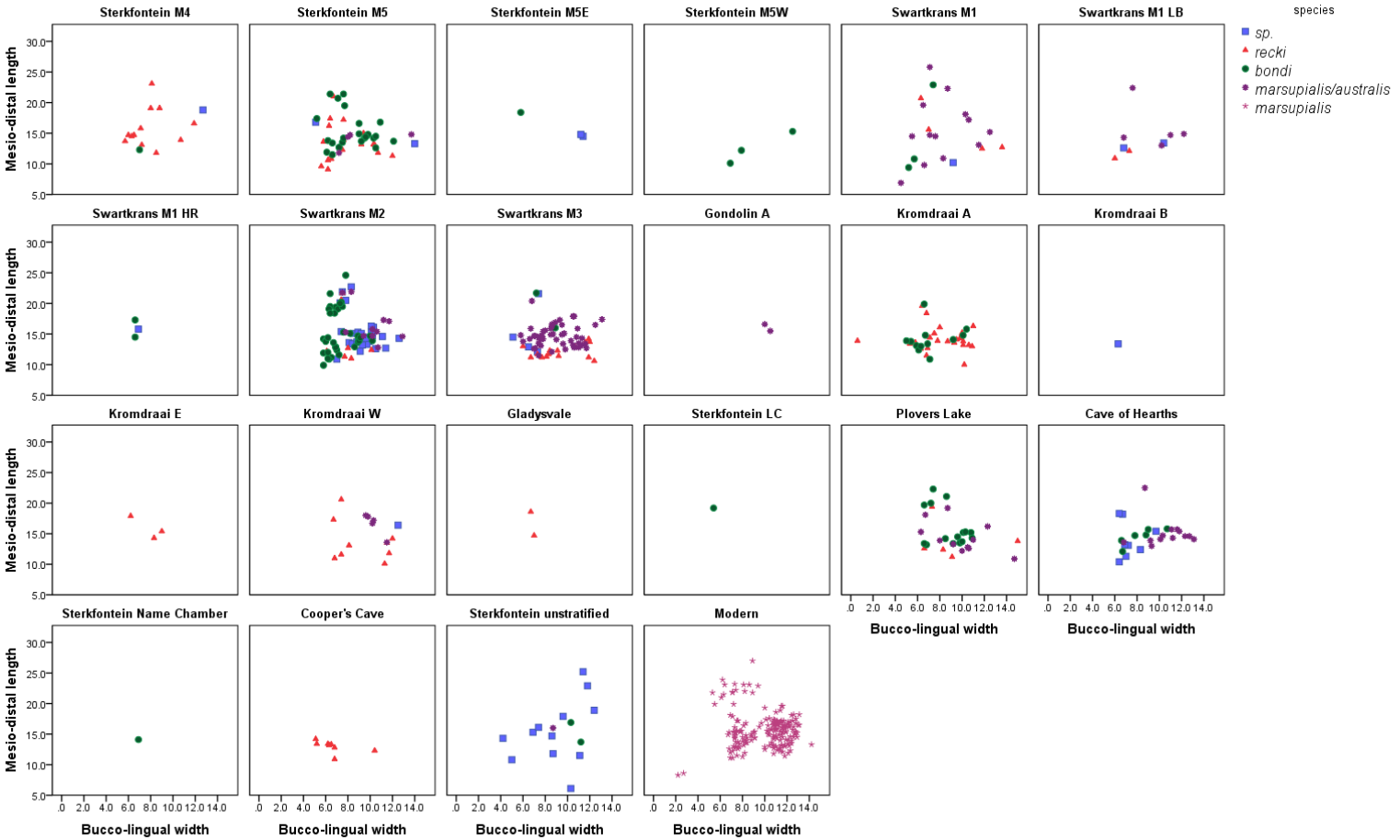


Figure 7.2: Measurement dimensions (BLW x MDL) scatter plots for all species of Antidorcas, separated according to site and member (provenance).

Further Statistical Analysis for *Antidorcas* Dental Enamel Thickness

As enamel thickness may reflect dietary abrasiveness and has been considered relatively sparingly in the past, special attention will be given to these measurements here.

Dentition is separated according to tooth type for analysis as significant differences in enamel thickness were found across the tooth row. For maxillary second molars (UM2), enamel thickness C is found to be significantly different across provenance categories via an Independent samples Kruskal-Wallis Test (p=0.013). For all other molars considered and for UM2 (locations A, B and D) no significant differences were found across provenance categories for any *Antidorcas* species.

Post-hoc *Antidorcas* enamel thickness difference through time

An independent samples Mann-Whitney U-test allowed for direct comparisons of each provenance, showing significant differences for the following: Sterkfontein Member 5 (n=8) *Antidorcas* enamel is thicker (mean=0.89mm) than at Swartkrans Member 1 (n=1) (mean=0.50mm) p=0.022; Sterkfontein Member 5 *Antidorcas* enamel is thicker than at Swartkrans Member 2 (n=10) (mean=0.59mm) p= 0.000; Sterkfontein Member 5 *Antidorcas* enamel is thicker than at Swartkrans Member 3 (n=12) (mean=0.71mm) p= 0.045; Sterkfontein Member 5 *Antidorcas* enamel is thicker than at Kromdraai A (n= 12) (mean=0.61mm) p=0.000; Sterkfontein Member 5 *Antidorcas* enamel is thicker than at Kromdraai W (n=4) (mean=0.65mm) p= 0.025; Sterkfontein Member 5 *Antidorcas* enamel is thicker than modern *A. marsupialis* (n=20) (mean=0.71mm) p=0.001; Swartkrans Member 2 (n=10) *Antidorcas* enamel is thinner than at Plovers Lake (n=10) (mean=0.82mm) p=0.011; Swartkrans Member 2 *Antidorcas* enamel is thinner than modern *A. marsupialis* (n=20) p=0.021; Kromdraai A (n=12) *Antidorcas* enamel is thinner than at Plovers Lake (n=10) p=0.006; Kromdraai A *Antidorcas* enamel is thinner than modern *A. marsupialis* (20) p=0.020.

It is possible that this difference across provenance is due to the morphological enamel thickness between species as discussed below. For example, Sterkfontein Member 5 yields *Antidorcas* with significantly thicker enamel compared to other sites, such as Swartkrans Member 3. However, the *Antidorcas* specimens measured from Sterkfontein Member 5 are dominated by *Antidorcas bondi*, whereas the Swartkrans Member 3 measurements are predominantly from fossil *Antidorcas marsupialis*.

Antidorcas Species Enamel Thickness Differences

Testing the variance in enamel thickness between species showed significant differences, with variations across tooth types (see Table 7.19 and Table 7.20). Post-hoc Mann-Whitney U tests with Bonferroni adjusted significant levels were used to show where these significant differences between species were, these are detailed in Table 7.20 below.

Table 7.19: Significance levels (P values) from an Independent samples Kruskal-Wallis test comparing the difference between enamel thickness at 4 points across Antidorcas species, with significance level below 0.05. lm1, lm2 etc. denote the tooth type, A, B, C, D denote the location of the enamel thickness measurements taken.

	lm1	lm2	lm3	UM1	UM2	UM3
A	0.429	**0.043**	**0.021**	0.982	0.141	0.083
B	0.903	0.306	**0.033**	0.204	0.298	**0.049**
C	0.086	0.539	0.087	0.825	**0.018**	**0.021**
D	n/p	n/p	n/p	0.076	**0.010**	**0.026**

Table 7.20: Significant differences in enamel thickness, for each molar, between Antidorcas species, exact values given below table.

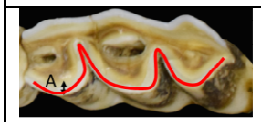
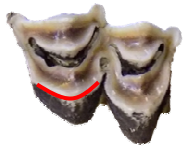
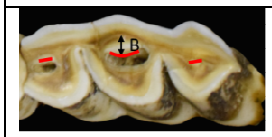
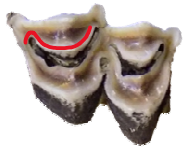
Measurement location		**lm1**	**lm2**	**lm3**		**UM1**	**UM2**	**UM3**
	**A**	No significant differences	*recki* and fossil *marsupialis*[1]; fossil *marsupialis* and modern *marsupials*[2]	*recki* and modern *marsupialis*[3] *bondi* and modern *marsupialis*[4]		No significant differences	No significant differences	
	**B**		No significant differences	sp. and *bondi*[5] sp. and fossil *marsupialiss*[6] *recki* and *bondi*[7]			No significant differences	*bondi* and fossil *marsupialis*[9]
	**C**		No significant differences				*recki* and *bondi*[8]	*recki* and *bondi*[10] *bondi* and fossil *marsupialis*[11]
	D	Not present					sp. and modern *marsupialis*[12] *recki* and *bondi*[13] *recki* and fossil *marsupialis*[14] fossil *marsupilias* and modern *marsupialis*[15]	*recki* and *bondi*[16] *bondi* and fossil *marsupialis*[17]

Table 10.20 values: [1]p=0.022 *A. recki* n=24, fossil *A. marsupialis* n=17. [2]p=0.008 fossil *A. marsupialis* n=17, modern *A. marsupialis* n=13. [3]p=0.008 A. recki n=19, modern *A. marsupialis* n=13. [4]p=0.002 *A. bondi* n=15, modern *A. marsupialis* n=13. [5]p=0.010 *Antidorcas* sp. n=3, *A. bondi* n=5. [6]p=0.031 *Antidorcas* sp. n=3, fossil *A. marsupialis* n=3. [7]p=0.022 *A. recki* n=10, *A. bondi* n=5. [8]p=0.005 *A. recki* n=19, *A. bondi* n=22. [9]p=0.004 *A. bondi* n=9, fossil *A. marsupialis* n=8. [10]p=0.024 *A. recki* n=8, *A. bondi* n=9. [11]p=0.002 *A. bondi* n =9, fossil *A. marsupialis* n=9. [12]p=0.033 *Antidorcas* sp. n=3, modern *A. marsupialis* n=19. [13]p=0.004 *A. recki* n=14, *A. bondi* n=21. [14]p=0.000 *A. recki* n=14, modern *A. marsupialis* n=19. [15]p=0.045 fossil *A. marsupialis* n=22, modern *A. marsupialis* n=19. [16]p=0.016 *A. recki* n=7, *A. bondi* n=9. [17]p=0.005 *A. bondi* n=9, fossil *A. marsupialis* n=9.

Antidorcas bondi had significantly thicker dental enamel at locations 'C' (mean=0.900mm) and 'D' (mean=1.578mm) than either *A. recki* (C mean=0.700mm; D mean=1.267mm) or fossil *A. marsupialis* (C mean=0.700mm; D mean=1.086mm) and at location 'B' (mean=1.067mm), significantly thicker than fossil *A. marsupialis* (mean=0.771mm). The thicker location 'D' reflects a larger mesostyle.

Enamel thickness on the internal enamel facet of the paracone of M^2 shows directional increase in thickness in Swartkrans from Member 1 to the younger, Member 3, with Member 3 being similar to the thickness of modern *A. marsupialis* paracone enamel. The thickest enamel is evident in Sterkfontein Member 5 (mean=0.89mm). There is quite considerable variation in enamel thickness (C) from members that fall into similar temporal ranges, Sterkfontein Member 5(all) (mean=0.89mm-thickest enamel), Swartkrans Member 2 (mean=0.59mm-thinnest enamel), Kromdraai A (mean=0.61mm) and Plovers Lake (mean=0.82mm).

7.2.4 Principal Component Analysis

Following from an initial Principal component analysis (PCA) attempt, small coefficients and unsuitable variables were removed from the factor analysis. Variables used in the PCA were MDL, BLW and all enamel thickness locations (EA, EB, EC and ED). The KMO test (Table 7.21) shows the data to be mediocre, and suitable for factor analysis (p=0.000). From this analysis (Figure 7.4, Figure 7.5), 'enamel thickness' and 'occlusal area' grouped as components. Initially the prevailing trend through time is given, this can highlight aspects such as increased dietary abrasion with greater enamel thickness. To ensure this 'enamel thickness' and 'occlusal area' are representative of change through time (Figure 7.5-Figure 7.6), rather than differential *Antidorcas* species presence, the following graphs are separated according to species (Figure 7.7-Figure 7.8).

Table 7.21: PCA results for UM2. A)KMO and Bartlett's Test for UM2 measurements with only suitable variables kept (MDL, BLW and enamel thickness at all locations measured). Data is shown to be mediocre (upper blue rectangle) and acceptable for factor analysis (lower blue rectangle). B) Data left in the factor analysis. Extraction method: Principal component analysis. C) Variance captured on each component (variables are kept on a component when the eigen value is higher than '1').

A) KMO and Bartlett's test

Kaiser-Meyer-Olkin Measure of Sampling Adequacy.		.698
Bartlett's Test of Sphericity	Approx. Chi-Square	255.674
	df	15
	Sig.	.000

B) Communalities

	Initial	Extraction
Mesio-distal length	1.000	.749
Bucco-lingual width	1.000	.455
Enamel Thickness A	1.000	.603
Enamel Thickness B	1.000	.673
Enamel Thickness C	1.000	.770
Enamel Thickness D	1.000	.413

C) Total Variance

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings			Rotation Sums of Squared Loadings		
	Total	% of variance	Cumulative %	Total	% of variance	Cumulative %	Total	% of variance	Cumulative %
1	2.490	41.506	41.506	2.490	41.506	41.506	2.475	41.245	41.245
2	1.171	19.509	61.015	1.171	19.509	61.015	1.186	19.770	61.015
3	.908	15.127	76.142						
4	.674	11.235	87.377						
5	.454	7.562	94.939						
6	.304	5.061	100.00						

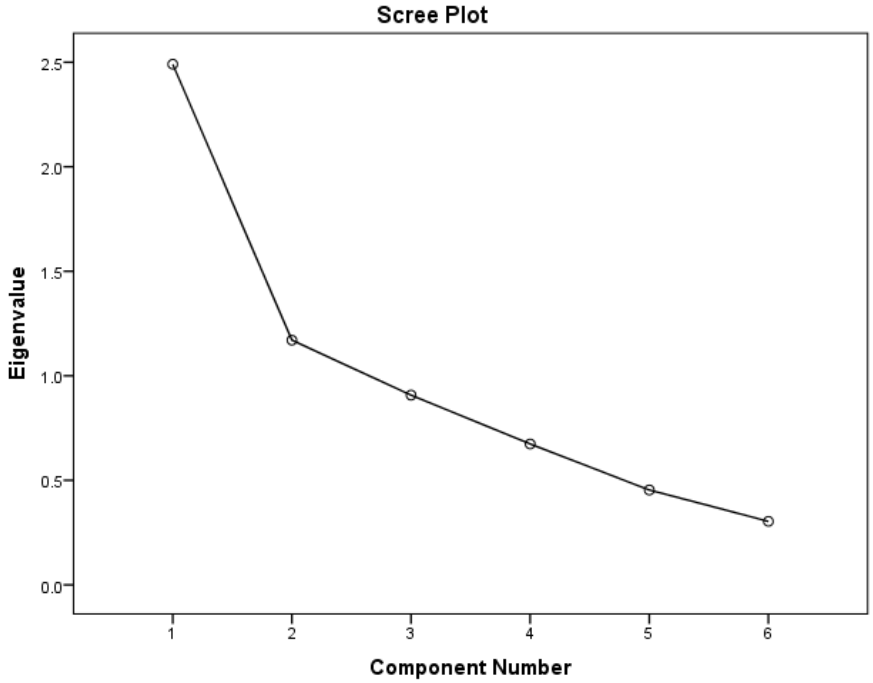


Figure 7.3: Principal component analysis on UM2 scree plot, visually displaying the components to keep in the analysis.

Table 7 22: Component matrix showing the loading of the variables with each component. Extraction method: Principal component analysis. 2 components extracted.

	Component	
	1	2
Enamel Thickness C	.875	
Enamel Thickness B	.796	
Enamel Thickness A	.776	
Enamel Thickness D	.613	
Mesio-distal length		.861
Bucco-lingual width		.590

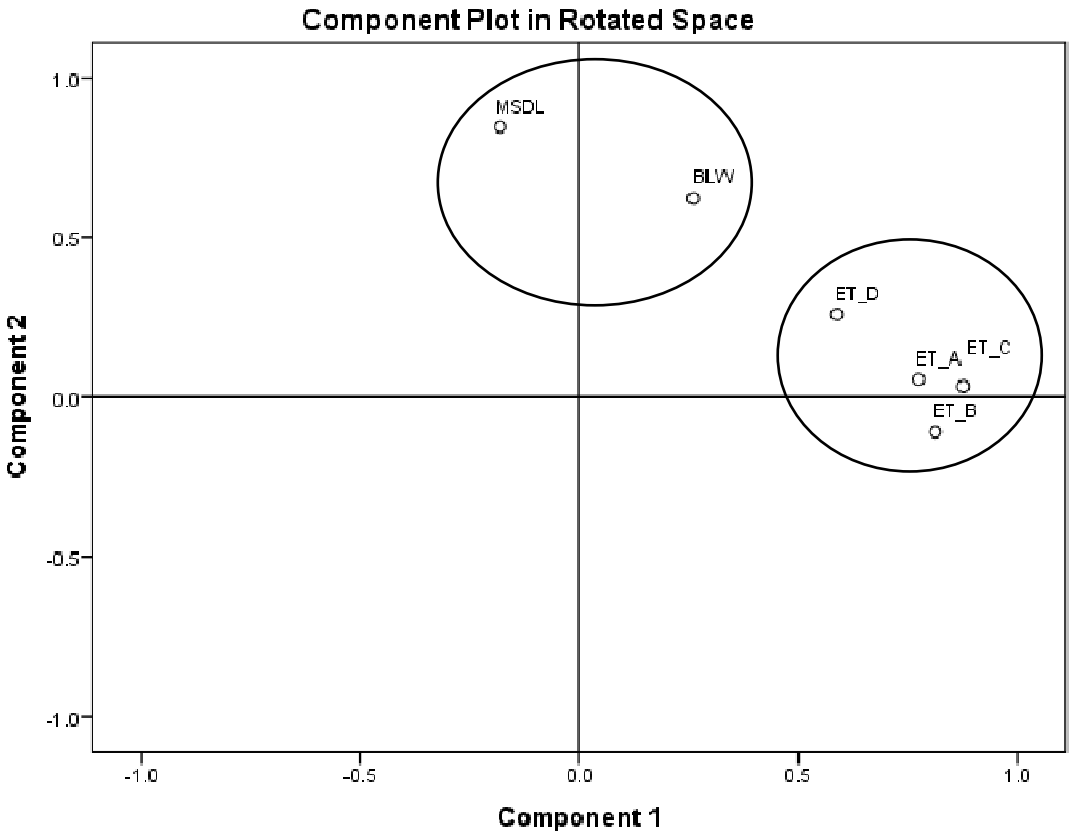


Figure 7.4: Principal component analysis results for Antidorcas dental molar (UM2) occlusal measurements

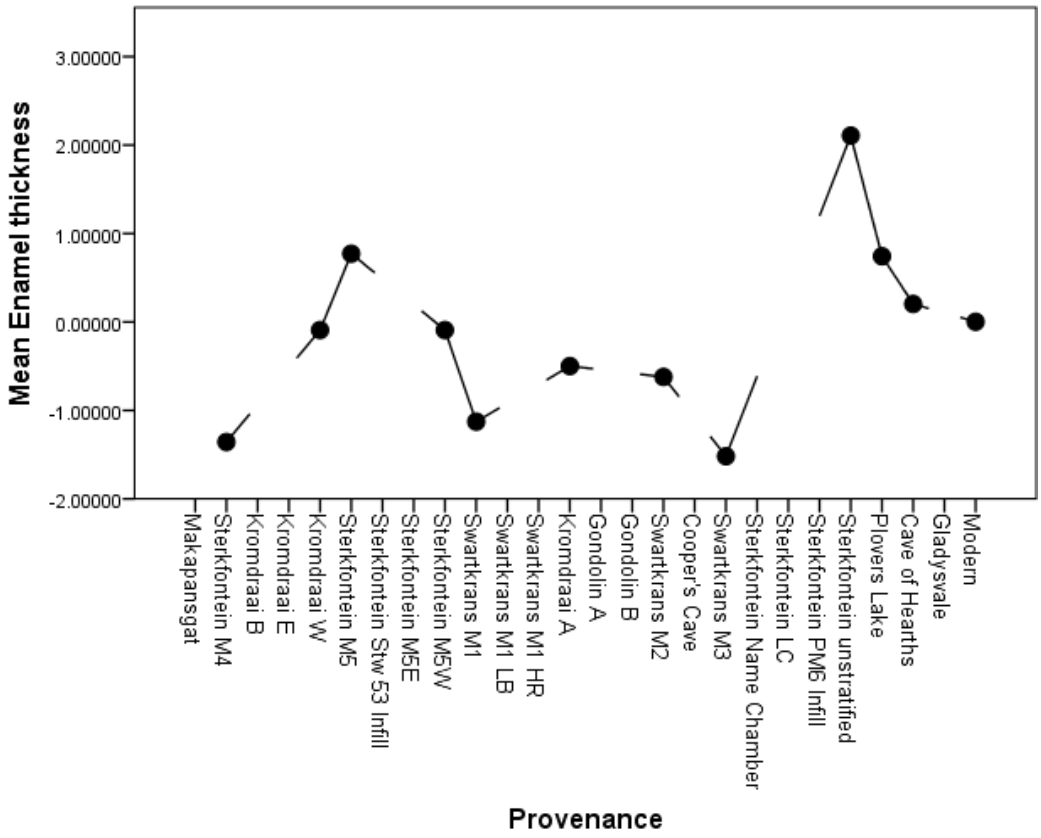


Figure 7.5: Mean enamel thickness (PCA component) through time c. 3Ma – 0.5 Ma and Modern, (chronologically ordered by provenance) for all Antidorcas (UM2). Breaks in the interpolation line show only where no data was collected.

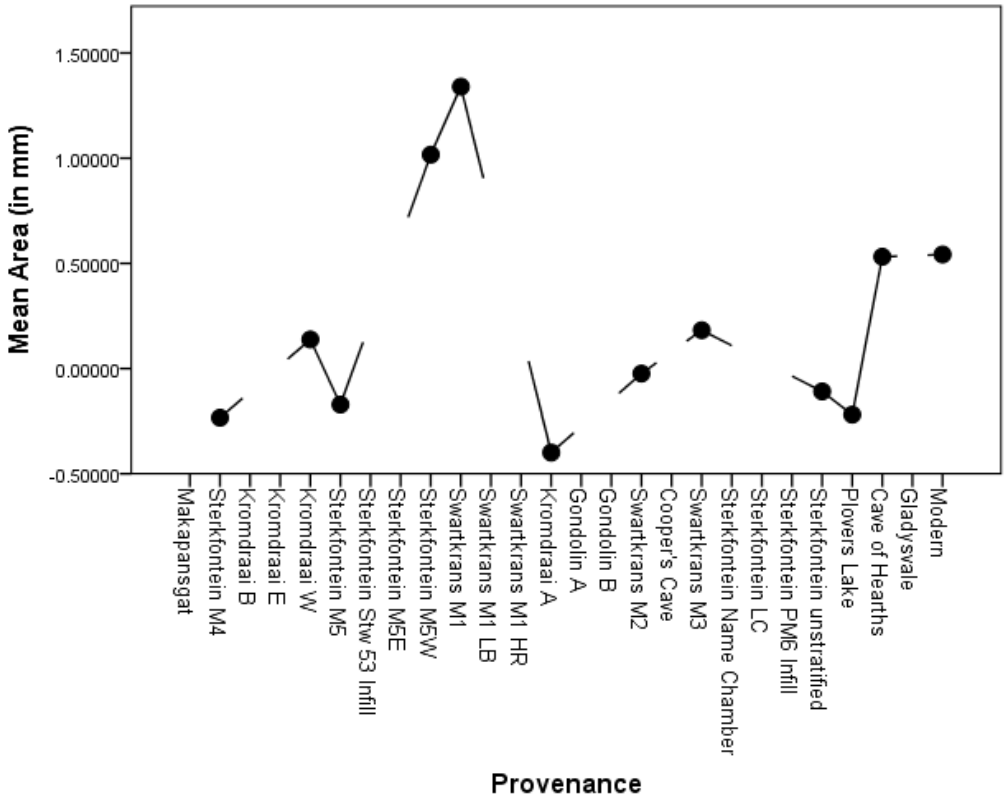


Figure 7.6: Mean occlusal area (PCA component, original measurements in mm, values not indicative of actual occlusal area) through time from c. 3.0-0.5 Ma and Modern, (chronologically ordered by provenance) for all Antidorcas (UM2). Breaks in the interpolation line show only where no data was collected.

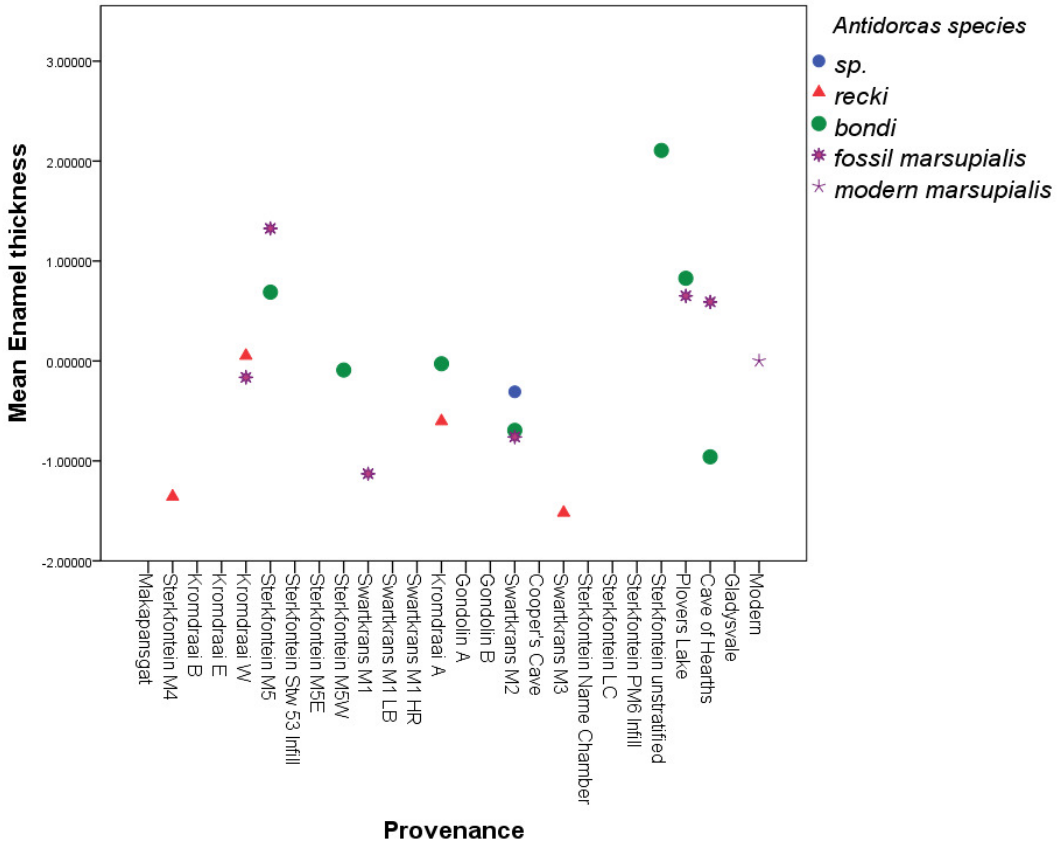


Figure 7.7: Mean enamel thickness (as a component, values not indicative of enamel thickness) through time (chronologically ordered provenance), as shown by each Antidorcas species.

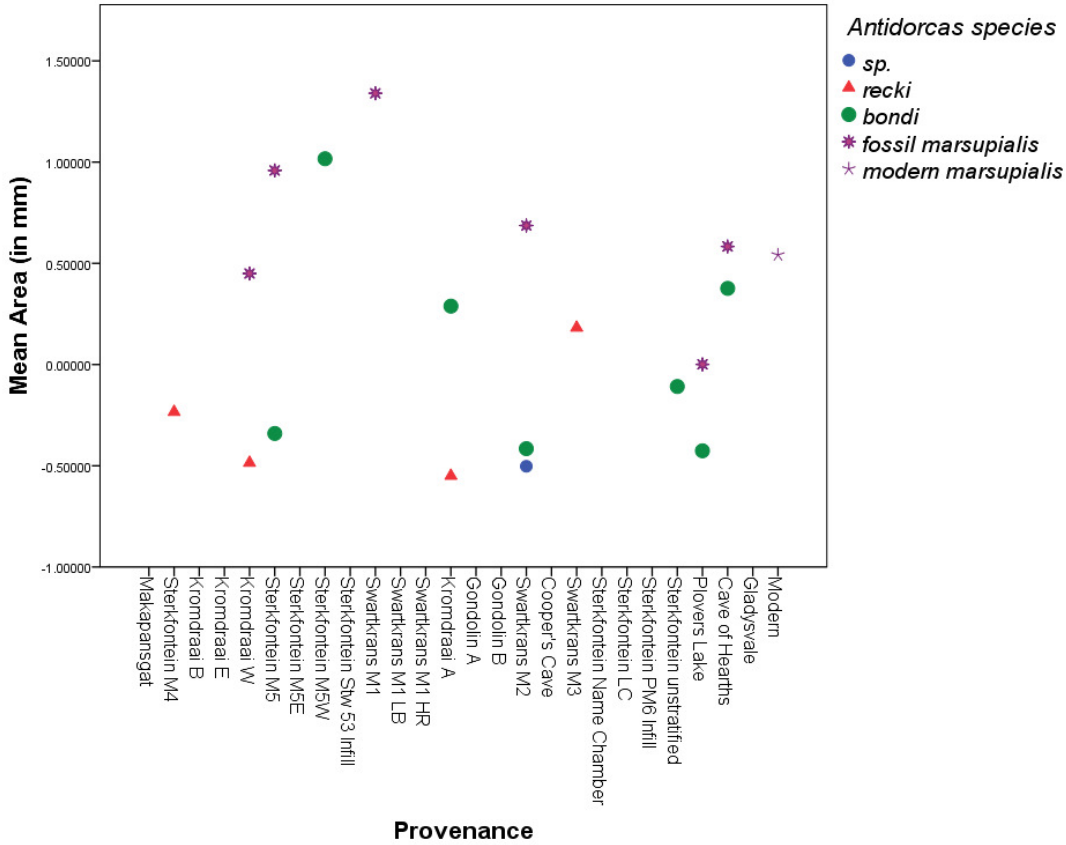


Figure 7.8:: Mean (UM2) occlusal area (as a component, original measurements in mm, values not indicative of actual occlusal area) through time (chronologically ordered provenance), as shown by each Antidorcas species.

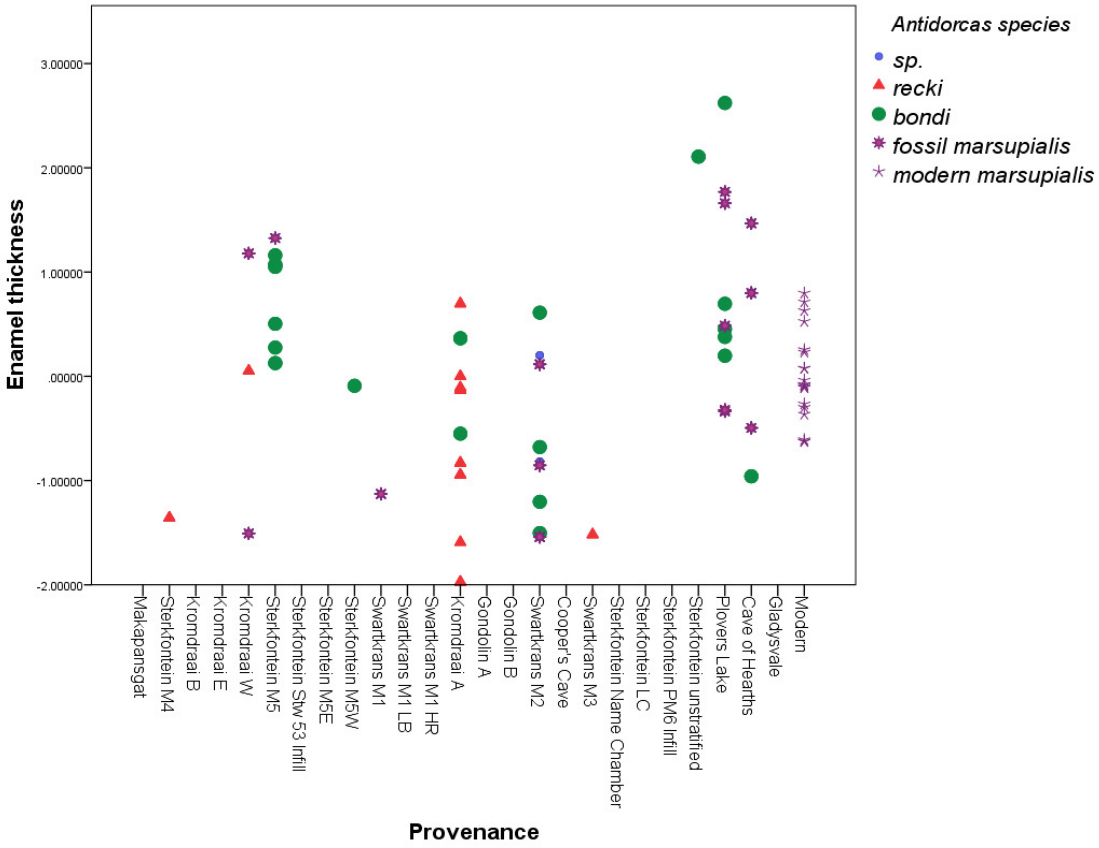


Figure 7.9: Enamel thickness (as a component, values are not representative of enamel thickness) through time (chronologically ordered provenance) for individuals within each Antidorcas species.

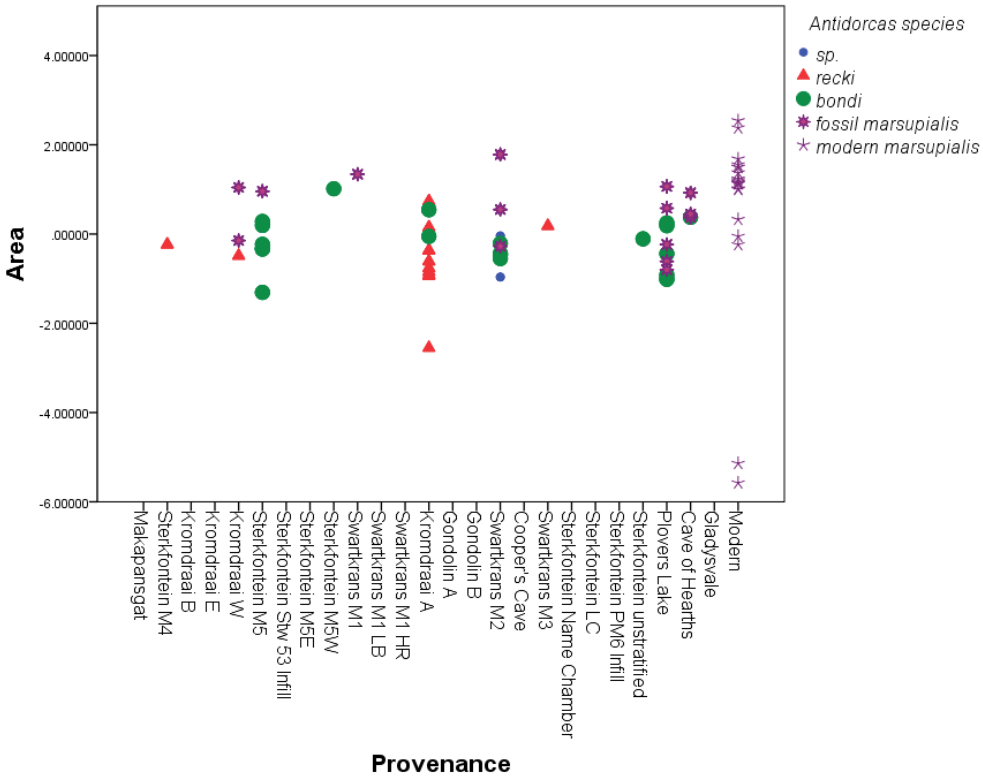


Figure 7.10: UM2 Occlusal area (as a component, values not indicative of actual occlusal area) through time (chronologically ordered provenance), as shown by each Antidorcas individual within a species.

Question: Do any of the *Antidorcas* species change dental size/shape through time/differ in any member? Does the genus as a whole change at all? What are the patterns of change?

Data Reduction: Dimension reduction was achieved via a principal component analysis (PCA). The derived components were sought to be reflective of overall tooth dimensions (incorporating all valid measurements taken), see Figure 7.4. 'Enamel thickness' was grouped in the principal component, with MDL and BLW converging on the second component as 'occlusal area' with 61% data captured. Enamel thickness measurements converged sufficiently to be seen as a reasonable component to take forward for analysis without considerable data loss.

An ANOVA considering 'enamel thickness' through time for all *Antidorcas* species was attempted but could not be run as this would break the assumption of homogeneity of variance. Therefore, a non-parametric independent samples kruskal-wallis test was carried out and showed significant differences for both enamel thickness (p=<.000) and occlusal area (p=<.000) through time for all *Antidorcas* species.

Post-hoc tests (conservative and non-conservative) were carried out to show where the significant differences were for each component (enamel thickness and occlusal area), and are detailed in Table 7.23 below.

Antidorcas morphology through time

When assessed at genus level, *Antidorcas* showed significant differences across provenance for enamel thickness and occlusal area, as detailed in Table 7.23.

Antidorcas species morphological differences through time

When split to consider *Antidorcas* species separately, *Antidorcas recki* did not show significant change in either component across provenance (site and stratigraphic site Member). However, *A. bondi* did show significant differences across provenance for enamel thickness (p=<.000) and occlusal area (p=<.000), as did fossil *A. marsupialis* for enamel thickness (p=<.000) and occlusal area (p=.003). Details of these significant differences are detailed in Table 7.23-Table 7.25. To reduce the impact of averaging, the trend for individuals within each species category was considered (see Figure 7.5-Figure 7.10).

Table 7.23: Antidorcas ET (enamel thickness component) P=<.0.00 and OV (occlusal area component) P=<.0.00, pairwise comparisons between provenance as evidenced by Tukeys HSD and Fishers LSD post-hoc tests. ET is shown above the line, OV below the line. Conservative significant differences are indicated in bold text. Significance is indicated below .05, with p values given in the table.

	SK M4	KW	SK M5	SK M5W	SKX M1	KA	SKX M2	SKX M3	PL	SK un.	COH	MDRN
SK M4		0.048	<.000; **.016**						.001; **.048**	<.000; **.006**	0.014	0.026
KW				0.017				0.026		0.006		
SK M5					<.000; **.032**	<.000; **<.000**	<.000; **<.000**	<.000; **.005**			0.03	0.004
SK M5 W			0.02							0.022		
SKX M1	0.026		0.005						0.001	<.000; **.011**	0.023	0.041
KA				0.004	0.001				<.000; **<.000**	<.000; **.003**	0.016	0.05
SKX M2				0.024	0.007				<.000; **<.000**	<.000; **.001**	0.008	0.024
SKX M3									<.000; **.017**	<.000; **.002**	0.006	0.013
PL				0.01	0.002							0.02
SK un.					0.045						0.01	0.004
COH			0.004			<.000; **.002**	0.004		<.000; **.029**			
MDRN	0.04	0.037	<.000; **.011**			<.000; **<.000**	<.000; **.009**		<.000; **<.000**			

Table 7.24: Antidorcas bondi ET (enamel thickness component) P=<.0.00, and OV (occlusal area component) P=<.0.00, pairwise comparisons between provenance as evidenced by Tukeys HSD and Fishers LSD post-hoc tests. ET is shown above the line, OV below the line. Conservative significant differences are indicated in bold text.

	SK M4	KW	SK M5	SK M5W	SKX M1	KA	SKX M2	SKX M3	PL	SK un.	COH
SK M4											
KW											
SK M5				0.041		0.041	<.000; **.005**				.001; **.037**
SK M5 W			0.003						0.05	0.003	
SKX M1											
KA			0.006							0.002	
SKX M2				<.000; **.012**		.001; **.015**			<.000; **.013**	<.000; **.001**	
SKX M3											
PL				.001; **.026**		.001; **.034**					0.002
SK un.											<.000; **.003**
COH			0.009				.001; **.032**		0.002		

Table 7.25: Antidorcas marsupialis OV (occlusal area component) P=<.0.00, and OV (occlusal area component) P=<.0.00, pairwise comparisons between provenance as evidenced by Tukeys HSD and Fishers LSD post-hoc tests. ET is shown above the line, OV below the line. Conservative significant differences are indicated in bold text.

	SK M4	KW	SK M5	SK M5W	SKX M1	KA	SKX M2	SKX M3	PL	SK un.	COH
SK M4											
KW									0.038		
SK M5					0.014		0.007				
SK M5 W											
SKX M1									0.005		0.025
KA											
SKX M2									<.000; **.003**		0.004
SKX M3											
PL		0.029	0.006		.001; **.014**		0.009				
SK un.											
COH					0.044				0.027		

7.3 DISCUSSION

Dental morphology is a reflection of the ancestral selection pressures exerted on the masticatory surfaces used to process vegetation to obtain sufficient nutrition and ensure species success. This chapter analysed the molar dimensions of *Antidorcas* species through time to attempt to see if, and when, any environmental stressors caused sufficient selective pressure to result in dental morphological adaptive evolution, and thereby potentially indicate palaeoenvironmental change being causally linked to faunal (*Antidorcas*) evolution.

The most likely explanation for the distinct groupings on both scatter plots (Figure 7.1-Figure 7.2) is sexual dimorphism. This dimorphic pattern is evident for the sites with greater sample sizes (Sterkfontein M5, Swartkrans M1, Swartkrans M2, Swartkrans M3, Kromdraai A and Plovers Lake) and cannot therefore be explained as difference through time or according to locality. This difference has been shown for modern springbok (see chapter 6) of known sex, which grouped reliably, according to sex. However, that the groupings are distinct across species, with little overlap between species (e.g. from large females of *A. recki* and small males of *A. marsupialis*) is unusual, it is possible that these groupings may represent populations of differing temporal range. Further exploration of this separation is an avenue for future work.

Antidorcas Species/Lineage Debate

As morphological measurements typically overlap for *Antidorcas* species, identifying speciation from morphological dimensions alone would be too unreliable.

Antidorcas bondi has significantly thicker enamel than either fossil *A. marsupialis* or *A. recki*, corroborating what would be expected of a highly abrasive diet (similar to that found for fossil camels studied by Semprebon and Rivals 2010).

Cusp height (occlusal height) is related to mesowear relief measurements. That these measurements remain similar across species suggests a strong phylogenetic influence, rather than occlusal relief *simply* being indicative of diet (as found by Janis 1995; Semprebon and Rivals 2010; Williams and Kay 2001).

That each measurement is significantly different at some point between species (within the *Antidorcas* genus), supports not using *Antidorcas* as a bioproxy for faunal adaptation and evolutionary change *without prior knowledge* of *Antidorcas* taxonomic identification to species level with any assemblage.

Change through time

Horizontal movement during mastication for herbivores is in the bucco-lingual direction. Therefore, the apparent increase in bucco-lingual width (BLW) for lm_1 from Swartkrans Member 1 to Swartkrans Member 3 may be an indication of dietary adaptation for *A. marsupialis,* which relates to an increased surface for grinding vegetation to maximise cell wall destruction and nutrient acquirement.

Antidorcas bondi shows increased occlusal (cusp) height through time for all molars from Sterkfontein Member 5 (c 1.8-1.1 Ma based on Herries and Shaw 2011, ESR for all Sterkfontein Member 5 units combined) to Cave of Hearths (c. 0.6-0.4 Ma, Wadley and McNabb 2009). Whilst only some members show significant differences, occlusal height is

evidentially progressively getting slightly higher through time. This suggests there may have been selection acting upon *A. bondi* at a low but continuous level, reaching a threshold at the points where significant differences are apparent, at least by c. 0.6 Ma (Cave of Hearths). Occlusal height is related to mesowear occlusal relief measurements and may reflect dietary behavioural or phylogenetic morphology advancements incrementally through time. Where the durability (hypsodonty and enamel thickness) of *A. bondi* is retained, cusp height is believed to relate more to tooth function than tooth durability (Damuth & Janis 2011). Further, *A. bondi* is believed to be a low-level feeder, consuming the new grass shoots close to the ground (Brink & Lee-Thorp 1992). It is probable that this led to increased grit in the diet, assisting in the development of molars adapted to resist high rates of tooth wear.

Low tooth crown height limits the amount of abrasive material that can be consumed on a long term; yet it may also limit the individuals' ability to effectively process large quantities of browse (Damuth & Janis 2011).

The exponential increase in crown height in *A. marsupialis* is likely to be indicative of increased open grasslands (e.g. Janis & Fortelius 1988; Janis 1988, 1995; Damuth & Janis 2011). *Antidorcas marsupialis* crown height increases from c.1.7Ma (at Swartkrans Member 2) to c. 1.0 Ma (at Swartkrans Member 3) but decreases again by ca. 0.8-0.6 Ma (at Cave of Hearths). Although Cave of Hearths is geographically distanced from Swartkrans, measurements are comparable and fall within the range of variation of *A. marsupialis*.

The greatest diversity for all linear measurements and enamel thicknesses appears in Sterkfontein Member 5 (all) [c. 1.7-0.8 Ma], Swartkrans Member 2 [c. 1.7-1.07 Ma], Kromdraai A (all) [c. 2.0-1.6 Ma] and Plovers Lake [c. 1 Ma]. These Members cover a temporal range of c. 2.0-1.5 Ma. The possibility exists that this time period reflects one of environmental instability with dietary (vegetation) stressors acting upon the dentition, catalysing adaptation in *Antidorcas*.

Where significant differences in enamel thickness are noted, these do not appear to prevail through time for fossil *Antidorcas*. Rather, these differences appear to be due to inter-specific variations within the *Antidorcas* genus. Although a small sample size, *A. marsupialis* enamel thickness as a component (see

Figure 7.9 and Table 7.24) indicates an increasing enamel thickness trend through time. However, considering individual measurements of enamel thickness (individually from each location measured), for *A. marsupialis*, this trend is by no means conclusive. Modern sub-species measurements can range between 0.01 mm to 5 mm variation (Table 7.1), therefore where fossil change does not appear continuously directional, it may be more likely to reflect only sub-specific level variations.

To contribute assessment on theories such as Vrba's (1985) turnover pulse hypothesis, evidence of *Antidorcas* turnover would need to be apparent and able to be precisely pinpointed to a specific time period for the *Antidorcas* lineage, as evidenced by dental metrics. There are no obvious definitive turnover delineations. By c. 0.8-0.5 Ma, *A. recki* is extinct or absent from the Cradle of Humankind, with *A. bondi* and *A. marsupialis*

dominating the assemblages. However, there is no clear transition to *A. marsupialis* evident from these dental assemblages. Gradual speciation (as opposed to a punctuated/ turnover event) is inferred from the dental evidence.

Palaeoenvironment indicators

Antidorcas bondi cusp height increases through time from Sterkfontein M5. This may be representative of increasing grasslands, if a more abrasive diet selects for the development of increased cusp height to withstand the excessive wear associated with abrasive diets.

Hypsodonty palaeoenvironmental implications

Mixed-feeders in open habitats were found to have significantly higher crowned teeth than mixed-feeders in closed habitats (Janis 1988). This concept is supported by the *Antidorcas* data presented here. *Antidorcas marsupialis* crown height increase for Swartkrans Member 3 supports the notion of more open grassland prevalence during this temporal period. Increased abrasion in the diet could be caused by an increase in grazing. However, abrasion could come from an increase in soil intake due to feeding close to the ground. This is more likely for grazers in open habitats and has therefore been associated as a grazing ungulate trait. Yet higher durable molar adaptation such as increased crown height, or hypsodonty, can also occur in low-level browsers (Damuth & Janis 2011).

Modern *A. marsupialis* have been witnessed using natural 'licks' (e.g. Nagy & Knight 1994). This is alternatively known as geophagy and is often practiced to counteract the effects of toxic secondary compounds in browse (e.g. Ayotte et al. 2006). Therefore, increased soil consumption, and consequentially increased crown height, in this instance may be reflective of closed woodland dominance/ low-level browse presence. The possibility exists that fossil *A. marsupialis* were increasingly subject to seasonal mixed-feeding fluctuations between graze and browse, both grazing and browsing at low levels and both dietary practices making *A. marsupialis* subject to a highly abrasive diet.

Fossil *Antidorcas marsupialis* crown height significantly, albeit temporarily, increased from Swartkrans Member 2 (mean 8.45mm) to Swartkrans Member 3 (mean 14.86mm). By c. 0.6Ma (Cave of Hearths), crown height significantly reduced again (mean 10.27 mm) but not to the low crown heights evident in Swartkrans Member 2.

Corroboration with modern *Antidorcas*

Modern *A. marsupialis* falls within these (fossil intra-genera and -specific) ranges for crown height, with the sub-specific *A. m. angolensis* displaying characteristically lower crown heights than *A. m.* marsupialis (see chapter 6). The vegetation in Angola typically includes more woodland and forest-type habitats compared to that of the ranges occupied by *A. m. marsupialis* in South Africa, Namibia and Botswana (see Figure 7.11). Whilst *A. m. angolensis*' preferred habitat is likely to be the western semi-desert region, as a mixed-feeder, they are able to move around the landscape in search of fresh vegetation as the need arises.

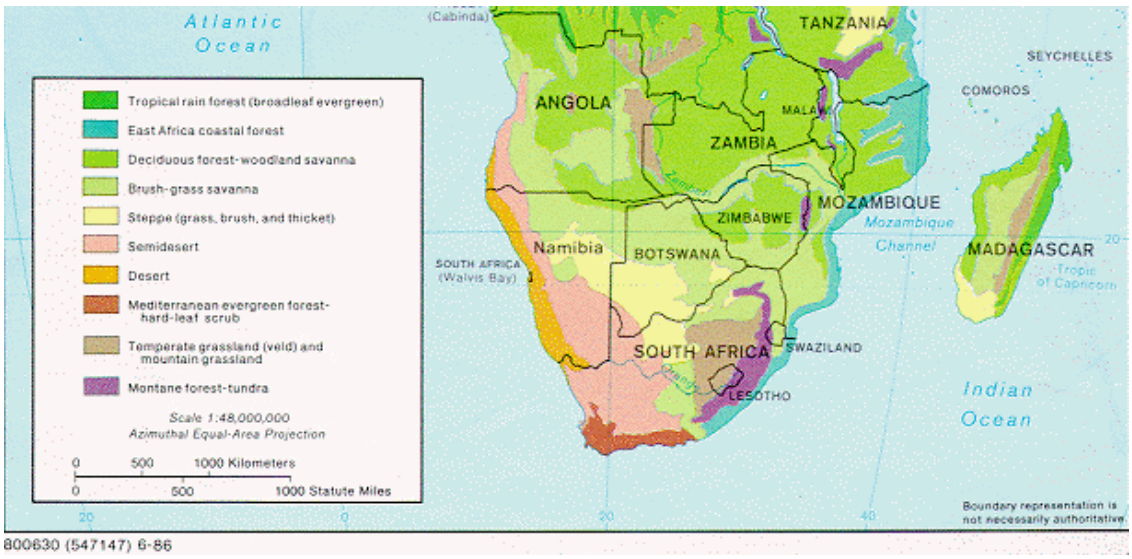


Figure 7.11: Modern vegetation map of southern Africa, edited from: https://www.mydigitalchalkboard.org/cognoti/content/file/resources/images/ee/eefd605d/eefd605dd966beedd655ba3e8cf1a828e872509a/downloadedfile_4257935605498713594_africa-veg.gif [accessed 04/06/2018: 10.01] to indicate differential modern vegetation cover for Angola (inhabited by A. m . angolensis) compared to South Africa, Botswana and Namibia.

7.4 SUMMARY

A relationship exists between diet and dental morphology. Change in this morphology is used here to inform on lineage change within the *Antidorcas* genus, as well as to infer palaeoenvironmental indicators from morphological changes inter- and intra- specifically for *Antidorcas* through time.

- *Antidorcas* through time: no definitive turnover event is apparent.
- *A. recki* shows no clear morphological change through time.
- *A. bondi* occlusal relief increases gradually through time, likely to withstand an increase in dietary abrasiveness (which supports Gailer and Kaiser 2014).
- *A. marsupialis* crown height gradually increases through time and BLW of lower first molar (lm_1) increased from Swartkrans Member 1 (c. 2.0-1.4 Ma) to Swartkrans Member 3 (c. 1.5-0.61 Ma).

CHAPTER 8

MESOWEAR

This chapter will introduce the concept of mesowear and the current use of mesowear to infer palaeodiets and, by inference, palaeovegetation present in the landscape. The method is reviewed and tested (see Appendix A7) before the *Antidorcas* data is analysed and discussed in regard to palaeodiet of the *Antidorcas* species and implications for paleoevegetation and changes therein through time.

8.1 INTRODUCTION

Building on discussions in previous chapters, animals mechanically process plants via mastication to rupture the cell walls in order to gain the essential nutrients from the plants (Sanson 2006). The properties of the plant (the cell walls of each plant type and plant part within) exert differing forces upon the surfaces chewing/grinding/shearing against them. The type of plant consumed on a regular basis, its abrasiveness to enamel and the extent to which the upper and lower dentition come into contact during this process results in wear of the dental occlusal surface. This level of wear is reflective of the averaged lifetime diet of an individual and is termed 'mesowear'(Fortelius and Solounias 2000, see chapter 4). Notwithstanding the various taphonomic issues associated with assemblage formations, higher numbers of browsers in an assemblage is believed to be indicative of more closed environments and woodland-type habitats, and more grazers of grasslands and savanna; and mixed feeders indicative of either seasonal or mixed environments (e.g. Vrba 1980; Janis 1995).

Mesowear is best used in conjunction with other methods, as a broad dietary indicator (Davis and Pineda-Munoz 2016; Louys et al. 2015) of an individual animal over its lifetime.

8.2 RESULTS

Tooth type and variation across the tooth row

Every mesowear variable showed significant differences across species and provenance before separating samples according to their tooth types. These apparent differences could be due to relative numbers of each dentition type within each sample. Therefore, all variables were checked for variation caused by the tooth measured (if causes of variation were due to the tooth being a 1st, 2nd or 3rd molar; being an upper or lower tooth; being left or right-sided and any combination of these, i.e. was mesowear likely to be different across the toothrow or within an individual). The following factors significantly impacted on mesowear variables (Table 8.1).

Table 8.1: Significant differences (Kruskal-Wallis test) in mesowear variables according to tooth type to assess which specimens can be analysed together. No significant differences were found to be dependent on whether the tooth was a 1st, 2nd or 3rd molar (upper and lower combined). Key: UM1= upper 1st molar, lm1=lower 1st molar; RUM1=right upper 1st molar, llm1=left lower first molar.

Dentition factor	Mesowear variable	Significance (p value)
Tooth (UM1, UM2, UM3, lm1, lm2, lm3)	Cusp shape	0.032
	New Mesowear 1-49	0.011
	New Relief	0.004
Maxillary/Mandibular	Mesowear 0-4	0.046
	Cusp shape	0.009
	Mesowear 1-6	0.038
	New Mesowear 1-49	0.007
	New Relief	0.001
	New cusp shape	0.029
	Mesowear III	0.047
Side (left/right)	Cusp shape	0.019
	New cusp shape	0.032
Tooth type (RUM1, RUM2, RUM3, LUM1, LUM2, LUM3, rlm1, rlm2, rlm3, llm1, llm2, llm3)	Cusp shape	0.022
	Mesowear 1-6	0.038

8.2.1 MODERN

Modern *A. marsupialis* shows typical mixed feeding signals with reasonably equal proportions of high and low relief. Blunt cusps appear relatively rarely (12%) for *Antidorcas*, however, the grazing, *Damaliscus pygargus* also yields relatively low percentage of blunt cusps and slightly higher percentages of high relief. This is perhaps unusual as grazing species would be expected to exhibit mesowear characteristics of low relief, blunt cusps predominantly, although rounded cusps can also be created from an abrasive (likely including a grazing element) diet.

Mesowear variables from modern specimens were tested for significance to establish firstly, the likely dietary parameters for grazers (*Damaliscus pygargus*), browsers (*Tragelaphus strepsiceros*) and mixed feeders (*Antidorcas marsupialis*), to better understand the mesowear dietary signals obtained from the fossil specimens (Table 8.2; see chapter 6). Secondly, modern mesowear variables were assessed for significant differences between tooth types to establish which fossil specimens could be grouped together to increase sample sizes (Table 8.1). No significant differences were found in mesowear variables along the toothrow, enabling all upper dentition to be grouped and all lower dentition to be grouped for analysis. Although this type of analysis of tooth type has been done before for other species (e.g. Kaiser and Solounias 2003), it had not been done for these particular taxa.

Table 8.2: Mesowear descriptive statistics (N= number of specimens; % of those scored in each category) for modern specimens (Antidorcas marsupialis and Damaliscus pygargus and Tragelaphus strepsiceros).

Species	Tooth type	**N (total)**	**N (low relief)**	**% Low Relief**	**N (High relief)**	**% High Relief**	**N (Blunt cusps)**	**% Blunt cusps**	**N (Rounded cusps)**	**% Rounded cusps**	**N (Sharp cusps)**	**% Sharp cusps**
Antidorcas marsupialis	UM1	39	22	56.4	17	43.6	4	10.3	19	48.7	16	41.0
	UM2	65	32	49.2	33	50.8	7	10.8	34	52.3	24	36.9
	UM3	7	0	0	7	100	1	14.3	1	14.3	5	71.4
	LM1	17	12	70.6	5	29.4	4	23.5	12	70.6	1	5.9
	LM2	32	18	56.3	14	43.8	4	12.5	16	50	12	37.5
	LM3	14	8	57.1	6	42.9	0	0	0	71.4	4	28.6
	M1	56	34	60.7	22	39.3	8	14.3	31	55.4	17	30.4
	M2	99	51	51.5	48	48.5	12	12.1	51	51.5	36	36.4
	M3	21	8	38.1	13	61.9	1	4.8	11	52.4	9	42.9
	Right	85	43	50.6	42	49.4	7	8.21	52	61.2	26	30.6
	Left	91	50	54.9	41	45.1	14	15.4	36	39.6	41	45.1
	Uppers	**112**	**55**	**49.1**	**57**	**50.9**	**12**	**10.7**	**55**	**49.1**	**45**	**40.2**
	Lowers	**64**	**38**	**59.4**	**26**	**40.6**	**9**	**14.1**	**38**	**59.4**	**17**	**26.6**
	RUM1	20	11	55	9	45	1	5	11	55	8	40
	RUM2	29	12	41.4	17	58.6	2	6.9	17	58.6	10	34.5
	RUM3	4	0	0	4	100	0	0	1	25	3	75
	LUM1	20	12	60	8	40	3	15	9	45	8	40
	LUM2	33	18	54.5	15	45.5	5	15.2	15	45.5	13	39.4
	LUM3	3	0	0	3	100	1	33.3	0	0	2	66.7
	RLM1	8	5	62.5	3	37.5	2	25	6.	75	0	0
	RLM2	15	9	60	6	40	2	13.3	9	60	4	26.7
	RLM3	6	4	66.7	2	33.3	0	0	6	100	4	26.7
	LLM1	9	7	77.8	2	22.2	2	22.2	6	66.7	1	11.1
	LLM2	17	9	52.9	8	47.1	3	17.6	6	35.3	8	47.1
	LLM3	9	4	44.4	5	55.6	0	0	5	55.6	4	44.4
Damaliscus	UM1	15	8	53.3	7	46.7	6	40	4	26.7	5	33.3

Species	Tooth type	N (total)	N (low	% Low	N (High	% High	N (Blunt	% Blunt	N (Rounded	% Rounded	N (Sharp	% Sharp
pygargus	UM2	37	26	70.3	11	29.7	22	59.5	11	29.7	4	10.8
	UM3	2	0	0	2	100	0	0	0	0	2	100
	LM1	11	2	18.2	19	81.8	2	18.2	9	81.8	0	0
	LM2	18	7	38.8	11	61.1	7	38.8	9	50	2	11.1
	LM3	5	1	20	4	80	1	20	3	60	1	20
	M1	26	10	38.5	16	61.5	8	30.8	13	50	5	19.2
	M2	57	35	61.4	22	38.6	29	50.9	23	40.4	5	8.8
	M3	7	1	14.3	6	85.7	1	14.3	3	42.9	3	42.9
	Right	46	26	56.5	20	43.5	20	43.5	20	43.5	6	13.0
	Left	44	20	45.5	24	54.5	18	41	19	43.18	7	15.9
	Uppers	**56**	**35**	**62.5**	**21**	**37.5**	**28**	**50**	**18**	**32.1**	**10**	**17.9**
	Lowers	**35**	**12**	**34.3**	**23**	**65.7**	**10**	**28.6**	**22**	**62.9**	**3**	**8.6**
	RUM1	8	5	62.5	3	37.5	3	37.5	3	37.5	2	25
	RUM2	19	4	21.1	15	78.9	11	57.9	7	36.8	1	5.3
	RUM3	1	0	0	1	100	0	0	0	0	1	100
	LUM1	8	3	37.5	5	62.5	3	37.5	2	25	3	37.5
	LUM2	17	11	64.7	6	35.3	10	58.8	6	35.3	1	5.9
	LUM3	1	0	0	1	100	0	0	0	0	1	100
	RLM1	5	1	20	4	80	1	20	4	80	0	0
	RLM2	9	4	44.4	5	55.6	4	44.4	4	44.4	1	11.1
	RLM3	3	1	33.3	2	66.7	1	33.3	1	33.3	1	33.3
	LLM1	5	1	20	4	80	1	20	4	80	0	0
	LLM2	9	4	44.4	5	55.6	3	33.3	5	55.6	1	11.1
	LLM3	2	0	0	2	100	0	0	2	100	0	0
Tragelaphus strepsiceros	UM2	20	2	10	18	90	1	5	11	55	8	40
	LM2	17	1	5.9	16	94.1	1	5.9	14	41.2	9	52.9
	LM3	6	0	0	6	100	0	0	1	16.7	5	83.3
	Right	22	1	4.5	21	95.5	1	4.5	11	50	10	45.5
	Left	21	2	9.5	19	90.1	1	4.8	8	38.1	12	57.1

Species	Tooth type	N (total)	N (low	% Low	N (High	% High	N (Blunt	% Blunt	N (Rounded	% Rounded	N (Sharp	% Sharp
	Uppers	**20**	**2**	**10**	**18**	**90**	**1**	**5**	**11**	**55**	**8**	**40**
	Lowers	**23**	**1**	**4.35**	**22**	**95.65**	**1**	**4.35**	**8**	**34.78**	**14**	**60.87**
	RUM2	10	1	10	9	90	1	10	6	60	3	30
	LUM2	10	1	10	9	90	0	0	5	50	5	50
	RLM2	9	0	0	9	100	0	0	4	44.4	5	55.6
	LLM2	8	1	12.5	7	87.5	1	12.5	3	37.5	4	50
	RLM3	3	0	0	3	100	0	0	1	33.3	2	66.7
	LLM3	3	0	0	3	100	0	0	0	0	3	100
	M2	37	3	8.1	34	91.9	2	5.4	18	48.6	17	45.9
	M3	6	6	100	0	0	0	0	1	16.7	5	83.3

8.2.1 FOSSIL

8.2.1.1 LOWER / MANDIBULAR DENTITION

Mesowear New Relief-table is provided in Appendices A7 as there were too many categories, creating false heightened levels of variation. All other results are presented here.

Antidorcas lineage (mandible)

All Members grouped together to analyse mesowear variables on mandibular dentition according to species to address the palaeoecology of species.

Table 8.3: Antidorcas species mandibular mesowear occlusal relief (left) and cusp shape (right). Percentages are rounded to 2 decimal places. LEFT: Number of individuals with high/low relief and their relevant percentages within the Antidorcas assemblage. RIGHT: Number of individuals with sharp/rounded/blunt cusps and their relevant percentages within the Antidorcas assemblage.

***Antidorcas* species**	Total N	High	**% High**	Low	**% Low**
sp.	42	8	**19**	34	**80.95**
recki	74	18	**24**	56	**75.68**
bondi	107	39	**36**	68	**63.55**

***Antidorcas* species**	Total N	High	**% High**	Low	**% Low**
fossil marsupialis	52	22	**42**	30	**57.69**
Modern *marsupialis*	68	28	**41**	40	**58.82**

Antidorcas species	Total N	Blunt	**% B**	Rounded	**% R**	Sharp	**% S**
sp.	42	9	**21**	22	**52**	11	**26.19**
recki	74	12	**16**	29	**39**	33	**44.59**
bondi	107	17	**16**	63	**59**	27	**25.23**
fossil marsupialis	52	7	**13**	25	**48**	20	**38.46**
Modern *marsupialis*	68	9	**13**	42	**62**	17	**25.00**

Table 8.4: Antidorcas species mandibular mesowear score (1-6), 1=LB, 2=LR,3=LS,4=HB,5=HR,6=HS. Percentages are rounded to 2 decimal places, Percentages are rounded to 2 decimal places where necessary.

Antidorcas species	Total N	LB	**%LB**	LR	**%LR**	LS	**%LS**	HB	**%HB**	HR	**%HR**	HS	**%HS**
sp.	42	9	**21**	16	**38**	9	**21**	0	**0**	6	**14**	2	**4.76**
recki	74	12	**16**	24	**32**	20	**27**	0	**0**	5	**7**	13	**17.57**
bondi	107	16	**15**	36	**34**	16	**15**	0	**0**	29	**27**	10	**9.35**
fossil marsupialis	52	7	**13**	13	**25**	10	**19**	0	**0**	12	**23**	10	**19.23**
Modern *marsupialis*	68	9	**13**	23	**34**	8	**12**	0	**0**	19	**28**	9	**13.24**

Table 8.5: Antidorcas species mandibular new mesowear relief. Number of individuals with high/medium/low relief and their relevant percentages within the Antidorcas assemblage. Percentages are rounded to 2 decimal places where necessary.

Antidorcas Species	Total N	High	**% High**	Medium	**% Medium**	Low	**%Low**
sp.	27	0	**0**	5	**19**	22	**81.48**
recki	65	4	**6**	15	**23**	46	**70.77**
bondi	58	5	**9**	20	**34**	33	**56.90**
fossil marsupialis	29	4	**14**	13	**45**	12	**41.38**
Modern *marsupialis*	69	11	**16**	38	**55**	20	**28.99**

Table 8.6: Antidorcas species mandibular new mesowear cusp shape. Number of individuals with each cusp shape category and their relevant percentages within the Antidorcas assemblage. Percentages are rounded to 2 decimal places where necessary.

Antidorcas species	Total N	Sharp	**% Sharp**	Sharp-Rounded	**% S-**	Rounded-Sharp	**%R-S**	Rounded	**%Rounded**	Rounded-Blunt	**%R-B**	Blunt-Rounded	**%B-R**	Blunt	**%Blunt**

					R										
sp.	27	3	**11**	5	**19**	4	**15**	4	**15**	5	**19**	2	**7**	4	**14.81**
recki	65	7	**11**	20	**31**	5	**8**	10	**15**	12	**18**	6	**9**	5	**7.69**
bondi	57	2	**4**	8	**14**	9	**16**	20	**35**	10	**18**	4	**7**	4	**7.02**
fossil marsupialis	28	3	**11**	11	**39**	5	**18**	7	**25**	2	**7**	0	**0**	0	**0.00**
Modern *marsupialis*	69	10	**14**	8	**12**	16	**23**	14	**20**	10	**14**	5	**7**	6	**8.70**

Palaeoenvironment (mandible)

Although tables 8.7 and 8.8 provide similar results, they highlight subtle differences. Most studies compare relative percentage of occlusal relief, and percentage of each cusp shape, as per Table 8.7. However, fewer researchers include the results combined, which appears more informative in providing additional palaeoecological subtleties (Table 8.8).

Table 8.7:Mesowear trend through time via Antidorcas lower mesowear relief and cusp shape. Number of individuals (N) with high/low relief and sharp/rounded/blunt cusps and their relevant percentages (%) within the Antidorcas assemblage. Percentages are rounded to 2 decimal places where applicable. SK=Sterkfontein, SKX=Swartkrans, K=Kromdraai, GL=Gladysvale, PL=Plovers Lake, CC=Cooper's Cave, CoH=Cave of Hearths, each provenance is listed with its relevant Member number/letter. 'unstrat'=unstratified.

Provenance	Total N	High	% High	Low	% Low	Total N	Blunt	% Blunt	Rounded	% Rounded	Sharp	% Sharp
SK M4	10	4	**40**	6	**60**	10	0	**0.00**	4	**40**	6	**60**
SK M5	29	4	**13.79**	25	**86.21**	29	5	**17.24**	15	**51.72**	9	**31.03**
SK M5 East	6	1	**16.67**	5	**83.33**	6	2	**33.33**	3	**50**	1	**16.67**
SK M5 West	12	0	**0**	12	**100**	12	3	**25**	8	**66.67**	1	**8.33**
SKX M1	10	6	**60**	4	**40**	10	3	**30**	5	**50**	2	**20**
SKX M1 LB	7	2	**28.57**	5	**71.43**	7	0	**0**	5	**71.43**	2	**28.57**
SKX M1 HR	3	0	**0**	3	**100**	3	0	**0**	2	**66.67**	1	**33.33**
SKX M2	63	27	**42.86**	36	**57.14**	63	9	**14.29**	40	**63.49**	14	**22.22**
SKX M 3	46	18	**39.13**	28	**60.87**	46	13	**28.26**	22	**47.83**	11	**23.91**

Provenance	Total N	High	% High	Low	% Low	Total N	Blunt	% Blunt	Rounded	% Rounded	Sharp	% Sharp
KA	19	2	**10.53**	17	**89.47**	19	1	**5.26**	6	**31.58**	12	**63.16**
KB	1	0	**0**	1	**100**	1	0	**0**	1	**100**	0	**0**
KE/D	2	0	**0**	2	**100**	2	0	**0**	0	**0**	2	**100**
KW	5	0	**0**	5	**100**	5	3	**60**	2	**40**	0	**0**
GL	2	0	**0**	2	**100**	2	0	**0**	1	**50**	1	**50**
SK LC	1	0	**0**	1	**100**	1	1	**100**	0	**0**	0	**0**
PL	13	2	**15.38**	11	**84.62**	13	2	**15.38**	4	**30.77**	7	**53.85**
CoH	33	17	**51.52**	16	**48.48**	33	1	**3.03**	19	**57.58**	13	**39.39**
SK Name Chamber	1	0	**0**	1	**100**	1	0	**0**	1	**100**	0	**0**
SK PM6 Infill	1	0	**0**	1	**100**	1	1	**100**	0	**0**	0	**0**
CC	7	4	**57.14**	3	**42.86**	7	1	**14.29**	1	**14.29**	5	**71.43**
SK unstrat	4	0	**0**	4	**100**	4	0	**0**	0	**0**	4	**100**
Modern	68	28	**41.18**	40	**58.82**	68	9	**13.24**	42	**61.76**	17	**25**

Table 8.8: Mesowear trend through time via Antidorcas lower mesowear scores 1-6. N=Total number of individuals. Number of individuals with high/low relief and sharp/rounded/blunt cusps and their relevant percentages within the Antidorcas assemblage. Percentages are rounded to 2 decimal places where applicable. SK=Sterkfontein, SKX=Swartkrans, K=Kromdraai, GL=Gladysvale, PL=Plovers Lake, CC=Cooper's Cave, CoH=Cave of Hearths, each provenance is listed with its relevant Member number/letter. 'unstrat'=unstratified. 'NC'=Name Chamber

Provenance	**N**	LB	**% LB**	LR	**% LR**	LS	**% LS**	HB	**% HB**	HR	**% HR**	HS	**% HS**
SK M4	10	0	**0**	3	**30**	3	**30**	0	0	1	**10**	3	**30**
SK M5	29	5	**17.24**	12	**41.38**	8	**27.59**	0	0	3	**10.34**	1	**3.45**
SK M5 East	6	2	**33.33**	2	**33.33**	1	**16.67**	0	0	1	**16.67**	0	**0**
SK M5 West	12	3	**25**	8	**66.67**	1	**8.33**	0	0	0	**0**	0	**0**
SKX M1	10	3	**30**	1	**10**	0	**0**	0	0	4	**40**	2	**20**
SKX M1 LB	7	0	**0**	4	**57.14**	1	**14.29**	0	0	1	**14.29**	1	**14.29**
SKX M1 HR	3	0	**0**	2	**66.67**	1	**33.33**	0	0	0	**0**	0	**0**
SKX M2	63	8	**12.70**	21	**33.33**	7	**11.11**	0	0	21	**33.33**	6	**9.52**
SKX M3	46	13	**28.26**	12	**26.09**	3	**6.52**	0	0	10	**21.74**	8	**17.39**
KA	19	1	**5.26**	6	**31.58**	10	**52.63**	0	0	0	**0**	2	**10.53**
KB	1	0	**0**	1	**100**	0	**0**	0	0	0	**0**	0	**0**
KE/D	2	0	**0**	0	**0**	2	**100**	0	0	0	**0**	0	**0**
KW	5	3	**60**	2	**40**	0	**0**	0	0	0	**0**	0	**0**
GL	2	0	**0**	1	**50**	1	**50**	0	0	0	**0**	0	**0**
SK LC	1	1	**100**	0	**0**	0	**0**	0	0	0	**0**	0	**0**
PL	13	2	**15.38**	4	**30.77**	5	**38.46**	0	0	0	**0**	2	**15.38**
CoH	33	1	**3.03**	8	**24.24**	7	**21.21**	0	0	11	**33.33**	6	**18.18**
SK NC	1	0	**0**	1	**100**	0	**0**	0	0	0	**0**	0	**0**
SK PM6 Infill	1	1	**100**	0	**0**	0	**0**	0	0	0	**0**	0	**0**
CC	7	1	**14.29**	1	**14.29**	1	**14.29**	0	0	0	**0**	4	**57.14**
SK unstrat.	4	0	**0**	0	**0**	4	**100**	0	0	0	**0**	0	**0**
Modern	68	9	**13.24**	23	**33.82**	8	**11.76**	0	0	19	**27.94**	9	**13.24**

Table 8.9: Mesowear trend through time via Antidorcas lower new relief. N= Total number of individuals. Number of individuals with high/medium/low occlusal relief and their relevant percentages within the Antidorcas assemblage. Percentages are rounded to 2 decimal places where applicable. SK=Sterkfontein, SKX=Swartkrans, K=Kromdraai, GL=Gladysvale, PL=Plovers Lake, CC=Cooper's Cave, CoH=Cave of Hearths, each provenance is listed with its relevant Member number/letter. 'unstrat'=unstratified.

Provenance	**N**	High	**% High**	Medium	**% Medium**	Low	**% Low**
SK M4	9	2	**22.22**	3	**33.33**	4	**44.44**
SK M5	29	3	**10.34**	5	**17.24**	21	**72.41**
SK M5 E	6	0	**0**	1	**16.67**	5	**83.33**
SK M5 W	11	0	**0**	2	**18.18**	9	**81.81**
SKX M1	4	1	**25**	1	**25**	2	**50**
SKX M1 LB	6	0	**0**	2	**33.33**	4	**66.67**

Provenance	**N**	High	**% High**	Medium	**% Medium**	Low	**% Low**
SKX M1 HR	3	0	**0**	2	**66.67**	1	**33.33**
SKX M2	32	3	**9.38**	11	**34.38**	18	**56.25**
SKX M3	29	4	**13.79**	10	**34.48**	15	**51.72**
KA	19	0	**0**	10	**52.63**	9	**47.37**
KB	1	0	**0**	0	**0**	1	**100**
KE/D	2	0	**0**	0	**0**	2	**100**
KW	5	0	**0**	0	**0**	5	**100**
GL	2	0	**0**	0	**0**	2	**100**
SK LC	1	0	**0**	0	**0**	1	**100**
PL	13	0	**0**	5	**38.46**	8	**61.54**
CoH	3	0	**0**	0	**0**	3	**100**
SK Name Chamber	1	0	**0**	0	**0**	1	**100**
SK PM6 Infill	1	0	**0**	0	**0**	1	**100**
SK unstrat.	2	0	**0**	1	**50**	1	**50**
Modern	69	11	**15.93**	38	**55.07**	20	**28.99**

Table 8.10: Mesowear trend through time via Antidorcas lower new cusp shape. N=Total number of individuals. 'S'=Sharp, 'R'=Rounded, 'B'=Blunt. Number of individuals with sharp/rounded/blunt cusps as divided by the new mesowear categories established here, and their relevant percentages within the Antidorcas assemblage. Percentages are rounded to 2 decimal places. SK=Sterkfontein, SKX=Swartkrans, K=Kromdraai, GL=Gladysvale, PL=Plovers Lake, CC=Cooper's Cave, CoH=Cave of Hearths, each provenance is listed with its relevant Member number/letter. 'unstrat'=unstratified.

Provenance	**N**	S	**% S**	S - R	**% S-R**	R - S	**% R-S**	R	**% R**	R - B	**% R-B**	B - R	**% B-R**	B	**%B**
SK M4	9	3	**33**	3	**33**	1	**11**	1	**11**	1	**11**	0	**0**	0	**0**
SK M5	29	1	**3**	8	**28**	1	**3**	7	**24**	7	**24**	1	**3**	4	**13.79**
SK M5 E	6	0	**0**	1	**17**	2	**33**	1	**17**	0	**0**	0	**0**	2	**33.33**
SK M 5 W	11	0	**0**	1	**9**	2	**18**	3	**27**	2	**18**	0	**0**	3	**27.27**
SKX M1	4	0	**0**	1	**25**	1	**25**	1	**25**	0	**0**	1	**25**	0	**0**
SKX M1 LB	6	0	**0**	2	**33**	0	**0**	4	**67**	0	**0**	0	**0**	0	**0**
SKX M1 HR	3	0	**0**	1	**33**	0	**0**	1	**33**	1	**33**	0	**0**	0	**0**
SKX M2	32	3	**9**	5	**16**	7	**22**	10	**31**	6	**19**	1	**3**	0	**0**
SKX M3	28	2	**7**	4	**14**	7	**25**	5	**18**	6	**21**	3	**11**	1	**3.57**
KA	19	2	**11**	10	**53**	0	**0**	3	**16**	3	**16**	1	**5**	0	**0**
KB	1	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**
KE/D	2	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
KW	5	0	**0**	0	**0**	0	**0**	0	**0**	2	**40**	2	**40**	1	**20**
GL	2	0	**0**	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**	0	**0**
SK LC	1	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**
PL	13	2	**15**	5	**38**	1	**8**	3	**23**	0	**0**	1	**8**	1	**7.69**
Cave of Hearths	3	0	**0**	1	**33**	0	**0**	1	**33**	0	**0**	1	**33**	0	**0**

Provenance	**N**	S	**% S**	S - R	**% S-R**	R - S	**% R-S**	R	**% R**	R - B	**% R-B**	B - R	**% B-R**	B	**%B**
SK Name Chamber	1	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
SK PM6 Infill	1	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**
SK unstrat.	1	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
Modern	69	10	**14**	8	**12**	16	**23**	14	**20**	10	**14**	5	**7**	6	**8.70**

Mesowear through time (Member), separated by species for mandibular molars

Table 8.11: Antidorcas mandibular dentition occlusal relief and cusp shape through time (per Member), shown in number of specimens per category and their respective percentages. Percentages rounded to two decimal places. Modern A. marsupialis given for comparison.

Antidorcas species	Provenance	Total N	High	**% High**	Low	**% Low**	Blunt	**% B**	Rounded	**% R**	Sharp	**% S**
sp.	Sterkfontein Member 5 East	3	0	**0**	3	**100**	2	**67**	1	**33**	0	**0**
	Sterkfontein Member 5 West	6	0	**0**	6	**100**	1	**17**	4	**67**	1	**16.67**
	Swartkrans Member 1 LB	1	1	**100**	0	**0**	0	**0**	1	**100**	0	**0**
	Swartkrans Member 1 HR	1	0	**0**	1	**100**	0	**0**	0	**0**	1	**100**
	Swartkrans Member 2	13	3	**23.08**	10	**76.92**	1	**8**	7	**54**	5	**38.46**
	Swartkrans Member 3	5	2	**40**	3	**60**	3	**60**	1	**20**	1	**20**
	Kromdraai B	1	0	**0**	1	**100**	0	**0**	1	**100**	0	**0**
	Cave of Hearths	8	2	**25**	6	**75**	1	**13**	7	**88**	0	**0**
	Sterkfontein PM6 Infill	1	0	**0**	1	**100**	1	**100**	0	**0**	0	**0**
	Sterkfontein unstratified	3	0	**0**	3	**100**	0	**0**	0	**0**	3	**100**
recki	Sterkfontein Member 4	8	4	**50**	4	**50**	0	**0**	2	**25**	6	**75**
	Sterkfontein Member 5	14	2	**14.29**	12	**85.71**	2	**14.29**	6	**42.86**	6	**42.86**
	Sterkfontein Member 5 East	1	0	**0**	1	**100**	0	**0**	1	**100**	0	**0**
	Sterkfontein Member 5 West	2	0	**0**	2	**100**	1	**50**	1	**50**	0	**0**
	Swartkrans Member 1	1	0	**0**	1	**100**	1	**100**	0	**0**	0	**0**
	Swartkrans Member 1 LB	3	0	**0**	3	**100**	0	**0**	3	**100**	0	**0**

Antidorcas species	Provenance	Total N	High	**% High**	Low	**% Low**	Blunt	**% B**	Rounded	**% R**	Sharp	**% S**
	Swartkrans Member 2	5	2	**40**	3	**60**	0	**0**	4	**80**	1	**20**
	Swartkrans Member 3	12	4	**33.33**	8	**66.67**	4	**33.33**	6	**50**	2	**16.67**
	Kromdraai A	10	2	**20**	8	**80**	0	**0**	2	**20**	8	**80**
	Kromdraai E/D	2	0	**0**	2	**100**	0	**0**	0	**0**	2	**100**
	Kromdraai W	5	0	**0**	5	**100**	3	**60**	2	**40**	0	**0**
	Gladysvale	2	0	**0**	2	**100**	0	**0**	1	**50**	1	**50**
	Plovers Lake	2	0	**0**	2	**100**	0	**0**	0	**0**	2	**100**
	Cooper's Cave	7	4	**57.14**	3	**42.86**	1	**14.29**	1	**14.29**	5	**71.43**
bondi	Sterkfontein Member 4	2	0	**0**	2	**100**	0	**0**	2	**100**	0	**0**
	Sterkfontein Member 5	12	1	**8.33**	11	**91.67**	3	**25**	8	**66.67**	1	**8.33**
	Sterkfontein Member 5 East	2	1	**50**	1	**50**	0	**0**	1	**50**	1	**50**
	Sterkfontein Member 5 West	4	0	**0**	4	**100**	1	**25**	3	**75**	0	**0**
	Swartkrans Member 1	3	2	**66.67**	1	**33.33**	1	**33.33**	2	**66.67**	0	**0**
	Swartkrans Member 1 LB	1	0	**0**	1	**100**	0	**0**	1	**100**	0	**0**
	Swartkrans Member 1 HR	2	0	**0**	2	**100**	0	**0**	2	**100**	0	**0**
	Swartkrans Member 2	42	21	**50**	21	**50**	8	**19.05**	26	**61.90**	8	**19.05**
	Swartkrans Member 3	2	1	**50**	1	**50**	0	**0**	2	**100**	0	**0**
	Kromdraai A	9	0	**0**	9	**100**	1	**11.11**	4	**44.44**	4	**44.44**

Antidorcas species	Provenance	Total N	High	**% High**	Low	**% Low**	Blunt	**% B**	Rounded	**% R**	Sharp	**% S**
	Sterkfontein LC	1	0	**0**	1	**100**	1	**100**	0	**0**	0	**0**
	Plovers Lake	6	0	**0**	6	**100**	2	**33.33**	2	**33.33**	2	**33.33**
	Cave of Hearths	20	13	**65**	7	**35**	0	**0**	9	**45**	11	**55**
	Sterkfontein Name Chamber	1	0	**0**	1	**100**	0	**0**	1	**100**	0	**0**
fossil marsupialis	Sterkfontein Member 5	3	1	**33.33**	2	**66.67**	0	**0**	1	**33.33**	2	**66.67**
	Swartkrans Member 1	6	4	**66.67**	2	**33.33**	1	**17**	3	**50**	2	**33.33**
	Swartkrans Member 1 LB	2	1	**50**	1	**50**	0	**0**	0	**0**	2	**100**
	Swartkrans Member 2	3	1	**33.33**	2	**66.67**	0	**0**	3	**100**	0	**0**
	Swartkrans Member 3	27	11	**40.74**	16	**59.26**	6	**22**	13	**48.15**	8	**29.63**
	Plovers Lake	5	2	**40**	3	**60**	0	**0**	2	**40**	3	**60**
	Cave of Hearths	5	2	**40**	3	**60**	0	**0**	3	**60**	2	**40**
	Sterkfontein unstratified	1	0	**0**	1	**100**	0	**0**	0	**0**	1	**100**
Modern *Antidorcas marsupialis*		68	28	**41.18**	40	**58.82**	9	**13**	42	**61.76**	17	**25**

Table 8.12: Antidorcas mandibular dentition mesowear scores through time (per Member), shown in number of specimens per category and their respective percentages. Percentages rounded to two decimal places. Modern A. marsupialis given for comparison.

Antidorcas species	Provenance	Total N	LB	**% LB**	LR	**% LR**	LS	**% LS**	HB	**% HB**	HR	**% HR**	HS	**% HS**
sp.	Sterkfontein Member 5 East	3	2	**67**	1	**33**	0	**0**	0	**0**	0	**0**	0	**0**
	Sterkfontein Member 5 West	6	1	**17**	4	**67**	1	**17**	0	**0**	0	**0**	0	**0**

Antidorcas species	Provenance	Total N	LB	**% LB**	LR	**% LR**	LS	**% LS**	HB	**% HB**	HR	**% HR**	HS	**% HS**
	Swartkrans Member 1 LB	1	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**
	Swartkrans Member 1 HR	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 2	13	1	**8**	5	**38**	4	**31**	0	**0**	2	**15**	1	**7.69**
	Swartkrans Member 3	5	3	**60**	0	**0**	0	**0**	0	**0**	1	**20**	1	**20**
	Kromdraai B	1	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	Cave of Hearths	8	1	**13**	5	**63**	0	**0**	0	**0**	2	**25**	0	**0**
	Sterkfontein PM6 Infill	1	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
	Sterkfontein unstratified	3	0	**0**	0	**0**	3	**100**	0	**0**	0	**0**	0	**0**
recki	Sterkfontein Member 4	8	0	**0**	1	**12.5**	3	**37.5**	0	**0**	1	**12.5**	3	**37.5**
	Sterkfontein Member 5	14	2	**14.29**	5	**35.71**	5	**35.71**	0	**0**	1	**7.14**	1	**7.14**
	Sterkfontein Member 5 East	1	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	Sterkfontein Member 5 West	2	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 1	1	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 1 LB	3	0	**0**	3	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 2	5	0	**0**	3	**60**	0	**0**	0	**0**	1	**20**	1	**20**
	Swartkrans Member 3	12	4	**33.33**	4	**33.33**	0	**0**	0	**0**	2	**16.67**	2	**16.67**
	Kromdraai A	10	0	**0**	2	**20**	6	**60**	0	**0**	0	**0**	2	**20**
	Kromdraai E/D	2	0	**0**	0	**0**	2	**100**	0	**0**	0	**0**	0	**0**

Antidorcas species	Provenance	Total N	LB	**% LB**	LR	**% LR**	LS	**% LS**	HB	**% HB**	HR	**% HR**	HS	**% HS**
	Kromdraai W	5	3	**60**	2	**40**	0	**0**	0	**0**	0	**0**	0	**0**
	Gladysvale	2	0	**0**	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**
	Plovers Lake	2	0	**0**	0	**0**	2	**100**	0	**0**	0	**0**	0	**0**
	Cooper's Cave	7	1	**14.29**	1	**14.29**	1	**14.29**	0	**0**	0	**0**	4	**57.14**
bondi	Sterkfontein Member 4	2	0	**0**	2	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	Sterkfontein Member 5	12	3	**25**	7	**58.33**	1	**8.33**	0	**0**	1	**8.33**	0	**0**
	Sterkfontein Member 5 East	2	0	**0**	0	**0**	1	**50**	0	**0**	1	**50**	0	**0**
	Sterkfontein Member 5 West	4	1	**25**	3	**75**	0	**0**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 1	3	1	**33.33**	0	**0**	0	**0**	0	**0**	2	**66.67**	0	**0**
	Swartkrans Member 1 LB	1	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 1 HR	2	0	**0**	2	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 2	42	7	**16.67**	11	**26.19**	3	**7.14**	0	**0**	17	**40.48**	4	**9.52**
	Swartkrans Member 3	2	0	**0**	1	**50**	0	**0**	0	**0**	1	**50**	0	**0**
	Kromdraai A	9	1	**11.11**	4	**44.44**	4	**44.44**	0	**0**	0	**0**	0	**0**
	Sterkfontein LC	1	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
	Plovers Lake	6	2	**33.33**	2	**33.33**	2	**33.33**	0	**0**	0	**0**	0	**0**
	Cave of Hearths	20	0	**0**	2	**10**	5	**25**	0	**0**	7	**35**	6	**30**
	Sterkfontein Name Chamber	1	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**

Antidorcas species	Provenance	Total N	LB	**% LB**	LR	**% LR**	LS	**% LS**	HB	**% HB**	HR	**% HR**	HS	**% HS**
fossil marsupialis	Sterkfontein Member 5	3	0	**0**	0	**0**	2	**66.67**	0	**0**	1	**33.33**	0	**0**
	Swartkrans Member 1	6	1	**16.67**	1	**16.67**	0	**0**	0	**0**	2	**33.33**	2	**33.33**
	Swartkrans Member 1 LB	2	0	**0**	0	**0**	1	**50**	0	**0**	0	**0**	1	**50**
	Swartkrans Member 2	3	0	**0**	2	**66.67**	0	**0**	0	**0**	1	**33.33**	0	**0**
	Swartkrans Member 3	27	6	**22.22**	7	**25.93**	3	**11.11**	0	**0**	6	**22.22**	5	**18.52**
	Plovers Lake	5	0	**0**	2	**40**	1	**20**	0	**0**	0	**0**	2	**40**
	Cave of Hearths	5	0	**0**	1	**20**	2	**40**	0	**0**	2	**40**	0	**0**
	Sterkfontein unstratified	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
Modern *Antidorcas marsupialis*		68	9	**13.24**	23	**33.82**	8	**11.76**	0	**0**	19	**27.94**	9	**13.24**

Table 8.13: Antidorcas sp. mandibular dentition new occlusal relief categories through time (per Member), shown in number of specimens per category and their respective percentages. Percentages rounded to two decimal places. Modern A. marsupialis given for comparison.

Antidorcas species	Provenance	Total N	High	**% H**	Medium	**% M**	Low	**% L**
sp.	Sterkfontein Member 5 East	3	0	**0**	0	**0**	3	**100**
	Sterkfontein Member 5 West	6	0	**0**	1	**16.67**	5	**83.33**
	Swartkrans Member 1 HR	1	0	**0**	1	**100**	0	**0**
	Swartkrans Member 2	11	0	**0**	2	**18.18**	9	**81.82**
	Swartkrans Member 3	1	0	**0**	1	**100**	0	**0**
	Kromdraai B	1	0	**0**	0	**0**	1	**100**
	Cave of Hearths	2	0	**0**	0	**0**	2	**100**

Antidorcas species	Provenance	Total N	High	% H	Medium	% M	Low	% L
	Sterkfontein PM6 Infill	1	0	**0**	0	**0**	1	**100**
	Sterkfontein unstratified	1	0	**0**	0	**0**	1	**100**
recki	Sterkfontein Member 4	7	2	**28.57**	2	**28.57**	3	**42.86**
	Sterkfontein Member 5	14	1	**7.14**	3	**21.43**	10	**71.43**
	Sterkfontein Member 5 East	1	0	**0**	0	**0**	1	**100**
	Sterkfontein Member 5 West	2	0	**0**	0	**0**	2	**100**
	Swartkrans Member 1	1	0	**0**	0	**0**	1	**100**
	Swartkrans Member 1 LB	3	0	**0**	0	**0**	3	**100**
	Swartkrans Member 2	5	0	**0**	2	**40**	3	**60**
	Swartkrans Member 3	11	1	**9.09**	3	**27.27**	7	**63.64**
	Kromdraai A	10	0	**0**	5	**50**	5	**50**
	Kromdraai E/D	2	0	**0**	0	**0**	2	**100**
	Kromdraai W	5	0	**0**	0	**0**	5	**100**
	Gladysvale	2	0	**0**	0	**0**	2	**100**
	Plovers Lake	2	0	**0**	0	**0**	2	**100**
bondi	Sterkfontein Member 4	2	0	**0**	1	**50**	1	**50**
	Sterkfontein Member 5	12	1	**8.33**	1	**8.33**	10	**83.33**
	Sterkfontein Member 5 East	2	0	**0**	1	**50**	1	**50**
	Sterkfontein Member 5 West	3	0	**0**	1	**33.33**	2	**66.67**
	Swartkrans Member 1	1	1	**100**	0	**0**	0	**0**

Antidorcas species	Provenance	Total N	High	% H	Medium	% M	Low	% L
	Swartkrans Member 1 LB	1	0	**0**	0	**0**	1	**100**
	Swartkrans Member 1 HR	2	0	**0**	1	**50**	1	**50**
	Swartkrans Member 2	16	3	**18.75**	7	**43.75**	6	**37.5**
	Swartkrans Member 3	2	0	**0**	1	**50**	1	**50**
	Kromdraai A	9	0	**0**	5	**55.56**	4	**44.44**
	Sterkfontein LC	1	0	**0**	0	**0**	1	**100**
	Plovers Lake	6	0	**0**	2	**33.33**	4	**66.67**
	Sterkfontein Name Chamber	1	0	**0**	0	**0**	1	**100**
fossil marsupialis	Sterkfontein Member 5	3	1	**33.33**	1	**33.33**	1	**33.33**
	Swartkrans Member 1	2	0	**0**	1	**50**	1	**50**
	Swartkrans Member 3	15	3	**20**	5	**33.33**	7	**46.67**
	Plovers Lake	5	0	**0**	3	**60**	2	**40**
	Cave of Hearths	1	0	**0**	0	**0**	1	**100**
Modern *Antidorcas marsupialis*		69	11	**15.94**	38	**55.07**	20	**28.99**

Table 8.14: Antidorcas sp. mandibular dentition new occlusal cusp shape categories through time (per Member), shown in number of specimens per category and their respective percentages. Percentages rounded to two decimal places where necessary. Normal text shows number of individuals ('N') displaying each mesowear type where, 'S' = sharp, 'S-R'=sharp-rounded, 'R-S' = Rounded-sharp, 'R' = Rounded, 'R-B'= Rounded-Blunt, 'B-R'= Blunt-Rounded, 'B' = Blunt. Bold text shows the percentage of each mesowear type. SK=Sterkfontein, SKX=Swartkrans, K=Kromdraai, GL=Gladysvale, PL=Plovers Lake, CC=Cooper's Cave, CoH=Cave of Hearths, each provenance is listed with its relevant Member number/letter. 'unstrat'=unstratified.

Species	Provenance	Total N	S	% S	S-R	% S-R	R-S	% R-S	R	% R	R-B	% R-B	B-R	% B-R	B	% B
sp.	SK M5 E	3	0	**0**	0	**0**	0	**0**	1	**33**	0	**0**	0	**0**	2	**66.67**

Species	Provenance	Total N	S	**% S**	S-R	**% S-R**	R-S	**% R-S**	R	**% R**	R-B	**% R-B**	B-R	**% B-R**	B	**% B**
	SK M5 W	6	0	**0**	1	**17**	2	**33**	1	**17**	1	**17**	0	**0**	1	**16.67**
	SKX M1 HR	1	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
	SKX M2	11	2	**18**	3	**27**	1	**9**	1	**9**	3	**27**	1	**9**	0	**0**
	SKX M3	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	KB	1	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**
	CoH	2	0	**0**	0	**0**	0	**0**	1	**50**	0	**0**	1	**50**	0	**0**
	SK PM6 Infill	1	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**
	SK unstrat.	1	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
recki	SK M4	7	3	**42.86**	3	**42.86**	0	**0**	1	**14.29**	0	**0**	0	**0**	0	**0**
	SK M5	14	1	**7.14**	5	**35.71**	1	**7.14**	4	**28.57**	1	**7.14**	0	**0**	2	**14.29**
	SK M5 E	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	SK M5 W	2	0	**0**	0	**0**	0	**0**	0	**0**	1	**50**	0	**0**	1	**50**
	SKX M1	1	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**
	SKX M1 LB	3	0	**0**	0	**0**	0	**0**	3	**100**	0	**0**	0	**0**	0	**0**
	SKX M2	5	0	**0**	1	**20**	1	**20**	1	**20**	2	**40**	0	**0**	0	**0**
	SKX M3	11	1	**9.09**	0	**0**	1	**9.09**	1	**9.09**	4	**36.36**	3	**27.27**	1	**9.09**
	KA	10	1	**10**	7	**70**	0	**0**	0	**0**	2	**20**	0	**0**	0	**0**
	KE/D	2	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
recki	K W	5	0	**0**	0	**0**	0	**0**	0	**0**	2	**40**	2	**40**	1	**20**
	GL	2	0	**0**	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**	0	**0**
	PL	2	0	**0**	2	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
bondi	SK M4	2	0	**0**	0	**0**	1	**50**	0	**0**	1	**50**	0	**0**	0	**0**

Species	Provenance	Total N	S	**% S**	S-R	**% S-R**	R-S	**% R-S**	R	**% R**	R-B	**% R-B**	B-R	**% B-R**	B	**% B**
	SK M5	12	0	**0**	1	**8.33**	0	**0**	2	**16.67**	6	**50**	1	**8.33**	2	**16.67**
	SK M5 E	2	0	**0**	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**	0	**0**
	SK M5 W	3	0	**0**	0	**0**	0	**0**	2	**66.67**	0	**0**	0	**0**	1	**33.33**
	SKS M1	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	SKX M1 LB	1	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
	SKX M1 HR	2	0	**0**	0	**0**	0	**0**	1	**50**	1	**50**	0	**0**	0	**0**
	SKX M2	16	1	**6.25**	1	**6.25**	5	**31.25**	8	**50**	1	**6.25**	0	**0**	0	**0**
	SKX M3	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	KA	9	1	**11.11**	3	**33.33**	0	**0**	3	**33.33**	1	**11.11**	1	**11.11**	0	**0**
	SK LC	1	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**
	PL	6	0	**0**	2	**33.33**	0	**0**	2	**33.33**	0	**0**	1	**16.67**	1	**16.67**
	SK Name Chamber	1	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
fossil marsupialis	SK M5	3	0	**0**	2	**66.67**	0	**0**	1	**33.33**	0	**0**	0	**0**	0	**0**
	SKX M1	2	0	**0**	1	**50**	0	**0**	1	**50**	0	**0**	0	**0**	0	**0**
	SKX M1 LB	2	0	**0**	2	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
	SKX M3	15	1	**6.67**	4	**26.67**	4	**26.67**	4	**26.67**	2	**13.33**	0	**0**	0	**0**
	PL	5	2	**40**	1	**20**	1	**20**	1	**20**	0	**0**	0	**0**	0	**0**
	CoH	1	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
Modern *A. marsupialis*		69	10	**14.49**	8	**11.59**	16	**23.19**	14	**20.29**	10	**14.49**	5	**7.25**	6	**8.70**

8.2.1.2 UPPER / MAXILLARY DENTITION

Antidorcas lineage (maxilla)

All Members are grouped together to analyse mesowear variables on maxillary dentition according to species, to address the palaeoecology of each *Antidorcas* species.

Table 8.15: Antidorcas species maxillary mesowear occlusal relief and cusp shape and percentages of each category. Percentages given to 2 decimal places where necessary.

Species	Total N	High	**% High**	Low	**% Low**	Blunt	**% B**	Rounded	**% R**	Sharp	**% S**
sp.	124	14	**11.29**	110	**88.71**	39	**31**	47	**38**	38	**30.65**
recki	63	7	**11.11**	56	**88.89**	19	**30**	18	**29**	26	**41.27**
bondi	97	20	**20.62**	77	**79.38**	11	**11**	52	**54**	34	**35.05**
fossil marsupialis	96	43	**44.79**	53	**55.21**	10	**10**	35	**36**	51	**53.13**
marsupialis (modern)	107	53	**49.53**	54	**50.47**	12	**11**	50	**47**	45	**42.06**

Table 8.16: Antidorcas species maxillary mesowear score (1-6). Percentages given to 2 decimal places where necessary.

Species	Total N	LB	**% LB**	LR	**% LR**	LS	**% LS**	HB	**% HB**	HR	**% HR**	HS	**% HS**
sp.	124	39	**31**	42	**34**	29	**23**	0	**0**	5	**4**	9	**7.26**
recki	63	19	**30**	15	**24**	22	**35**	0	**0**	3	**5**	4	**6.35**
bondi	97	11	**11**	37	**38**	29	**30**	0	**0**	15	**15**	5	**5.15**
fossil marsupialis	96	10	**10**	24	**25**	19	**20**	0	**0**	11	**11**	32	**33.33**
marsupialis (modern)	107	10	**9**	31	**29**	13	**12**	2	**2**	19	**18**	32	**29.91**

Table 8.17: Antidorcas species maxillary new mesowear relief. Percentages given to 2 decimal places where necessary.

Species	Total N	High	**% High**	Medium	**% Medium**	Low	**% Low**
sp.	97	0	**0**	19	**19.59**	78	**80.41**
recki	62	3	**4.84**	14	**22.58**	45	**72.58**
bondi	71	3	**4.23**	19	**26.76**	49	**69.01**
fossil marsupialis	59	9	**15.25**	15	**25.42**	35	**59.32**

marsupialis (modern)	105	30	**28.57**	54	**51.43**	21	**20**

Table 8.18: Antidorcas species maxillary new mesowear cusp shape. Percentages given to 2 decimal places where necessary.

Species	Total N	Sharp	**% S**	Sharp-Rounded	**% S-R**	Rounded-Sharp	**% R-S**	Rounded	**% R**	Rounded-Blunt	**% R-B**	Blunt-Rounded	**% B-R**	Blunt	**% B**
sp.	97	4	**4**	22	**23**	17	**18**	14	**14**	6	**6**	20	**21**	14	**14.43**
recki	62	5	**8**	19	**31**	8	**13**	4	**6**	7	**11**	11	**18**	8	**12.90**
bondi	71	5	**7**	22	**31**	15	**21**	12	**17**	8	**11**	5	**7**	4	**5.63**
fossil marsupialis	59	7	**12**	22	**37**	11	**19**	6	**10**	7	**12**	2	**3**	4	**6.78**
marsupialis (modern)	105	27	**26**	17	**16**	13	**12**	23	**22**	14	**13**	5	**5**	6	**5.71**

Table 8.19. Antidorcas species Mesowear III scores. Percentages given to 2 decimal places where necessary.

Species	Total N	1	**%1**	2	**%2**	3	**%3**	4	**%4**
sp.	5	1	**20**	0	**0**	3	**60**	1	**20**
recki	37	1	**2.70**	7	**18.92**	15	**40.54**	14	**37.84**
bondi	29	0	**0**	1	**3.45**	6	**20.69**	22	**75.86**
fossil marsupialis	40	2	**5**	9	**22.5**	15	**37.5**	14	**35**
marsupialis (modern)	19	6	**31.58**	6	**31.58**	6	**31.58**	1	**5.26**

Palaeoenvironment (maxilla)

Table 8.20: Mesowear trend through time via Antidorcas upper mesowear relief and cusp shape. Number of individuals with each category and their relevant percentages within the Antidorcas assemblage. Percentages are rounded to 2 decimal places where necessary . 'N' = total number of individuals.'H'=High, 'L'=Low, 'B'=Blunt, 'R'=Rounded, 'S'=Sharp. SK=Sterkfontein, SKX=Swartkrans, K=Kromdraai, GL=Gladysvale, PL=Plovers Lake, G=Gondolin, CC=Cooper's Cave, CoH=Cave of Hearths, each provenance is listed with its relevant Member number/letter. 'unstrat'=unstratified.

Provenance	N	H	**% H**	L	**% L**	B	**% B**	R	**% R**	S	**% S**
SK M4	3	1	**33.33**	2	**66.67**	0	**0**	2	**67**	1	**33.33**
SK M5	21	1	**4.76**	20	**95.24**	2	**9.52**	13	**62**	6	**28.57**
SK M5 E	2	0	**0**	2	**100**	0	**0**	0	**0**	2	**100**
SK M5 W	8	0	**0**	8	**100**	3	**37.5**	2	**25**	3	**37.5**
SKX M1	9	2	**22.22**	7	**77.78**	2	**22.22**	2	**22**	5	**55.56**
SKX M1 LB	5	4	**80**	1	**20**	0	**0**	0	**0**	5	**100**
SKX M2	191	25	**13.09**	166	**86.91**	56	**29.32**	71	**37**	64	**33.51**
SKX M3	58	30	**51.72**	28	**48.28**	9	**15.52**	26	**45**	23	**39.66**
GA	2	0	**0**	2	**100**	0	**0**	1	**50**	1	**50**
KA	16	1	**6.25**	15	**93.75**	0	**0**	8	**50**	8	**50**
KE/D	1	1	**100**	0	**0**	0	**0**	1	**100**	0	**0**
KW	11	5	**45.45**	6	**54.55**	1	**9.09**	3	**27**	7	**63.64**
PL	17	0	**0**	17	**100**	2	**11.76**	6	**35**	9	**52.94**
CoH	30	13	**43.33**	17	**56.67**	3	**10**	16	**53**	11	**36.67**
SK PM6 Infill	1	0	**0**	1	**100**	0	**0**	0	**0**	1	**100**
CC	1	0	**0**	1	**100**	0	**0**	0	**0**	1	**100**
SK unstrat.	4	1	**25**	3	**75**	1	**25**	1	**25**	2	**50**
Modern	107	53	**49.53**	54	**50.47**	12	**11.21**	50	**47**	45	**42.06**

Table 8.21: Mesowear trend through time via Antidorcas upper mesowear scores 1-6. Number of individuals with each category and their relevant percentages within the Antidorcas assemblage. 'N' = total number of individuals. Percentages are rounded to 2 decimal places where applicable. SK=Sterkfontein, SKX=Swartkrans, K=Kromdraai, GL=Gladysvale, PL=Plovers Lake, G=Gondolin, CC=Cooper's Cave, CoH=Cave of Hearths, each provenance is listed with its relevant Member number/letter. 'unstrat'=unstratified.

Provenance	N	LB	**% LB**	LR	**% LR**	LS	**% LS**	HB	**% HB**	HR	**% HR**	HS	**% HS**
SK M4	3	0	**0**	2	**67**	0	**0**	0	**0**	0	**0**	1	**33.33**
SK M5	21	2	**10**	12	**57**	6	**29**	0	**0**	1	**5**	0	**0**
SK M-5 E-	2	0	**0**	0	**0**	2	**100**	0	**0**	0	**0**	0	**0**
SK M5 W	8	3	**38**	2	**25**	3	**38**	0	**0**	0	**0**	0	**0**
SKX M1	9	2	**22**	1	**11**	4	**44**	0	**0**	1	**11**	1	**11.11**

Provenance	N	LB	**%LB**	LR	**%LR**	LS	**%LS**	HB	**%HB**	HR	**%HR**	HS	**%HS**
SKX M1 LB	5	0	**0**	0	**0**	1	**20**	0	**0**	0	**0**	4	**80**
SKX M2	191	56	**29**	58	**30**	52	**27**	0	**0**	13	**7**	12	**6.28**
SKX M3	58	9	**16**	15	**26**	4	**7**	0	**0**	11	**19**	19	**32.76**
GA	2	0	**0**	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**
KA	16	0	**0**	8	**50**	7	**44**	0	**0**	0	**0**	1	**6.25**
KE/D	1	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**
KW	11	1	**9**	3	**27**	2	**18**	0	**0**	0	**0**	5	**45.45**
PL	17	2	**12**	6	**35**	9	**53**	0	**0**	0	**0**	0	**0**
CoH	30	3	**10**	9	**30**	5	**17**	0	**0**	7	**23**	6	**20**
SK PM6 Infill	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
CC	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
SK unstrat.	4	1	**25**	1	**25**	1	**25**	0	**0**	0	**0**	1	**25**
Modern	107	10	**9**	31	**29**	13	**12**	2	**2**	19	**18**	32	**29.91**

Table 8.22: Mesowear trend through time via Antidorcas upper new relief. Number of individuals with each category and their relevant percentages within the Antidorcas assemblage. Percentages are rounded to 2 decimal places where necessary. SK=Sterkfontein, SKX=Swartkrans, K=Kromdraai, GL=Gladysvale, PL=Plovers Lake, G=Gondolin, CC=Cooper's Cave, CoH=Cave of Hearths, each provenance is listed with its relevant Member number/letter. 'unstrat'=unstratified.

Provenance	Total N	High	**% H**	Medium	**% M**	Low	**% L**
SK M4	3	0	**0**	1	**33.33**	2	**66.67**
SK M5	21	0	**0**	5	**23.81**	16	**76.19**
SK M5 E	2	0	**0**	0	**0**	2	**100**
SK M5 W	8	1	**12.5**	2	**25**	5	**62.5**
SKX M1	6	0	**0**	3	**50**	3	**50**
SKX M1 LB	2	0	**0**	1	**50**	1	**50**
SKX M2	161	4	**2.48**	32	**19.88**	125	**77.64**
SKX M3	32	6	**18.75**	10	**31.25**	16	**50**
GA	2	0	**0**	0	**0**	2	**100**
KA	16	0	**0**	4	**25**	12	**75**
KE/D	1	0	**0**	1	**100**	0	**0**
KW	11	4	**36.36**	3	**27.27**	4	**36.36**
PL	17	0	**0**	3	**17.65**	14	**82.35**
CoH	4	0	**0**	2	**50**	2	**50**
SK PM6 Infill	1	0	**0**	0	**0**	1	**100**
SK unstrat.	2	0	**0**	0	**0**	2	**100**
Modern	105	30	**28.57**	54	**51.43**	21	**20**

Table 8.23: Mesowear trend through time via Antidorcas upper new cusp shape. Number of individuals with each category and their relevant percentages within the Antidorcas assemblage. Percentages are rounded to 2 decimal places where necessary. SK=Sterkfontein, SKX=Swartkrans, K=Kromdraai, GL=Gladysvale, PL=Plovers Lake, G=Gondolin, CC=Cooper's Cave, CoH=Cave of Hearths, each provenance is listed with its relevant Member number/letter. 'unstrat'=unstratified.

Provenance	Total N	Sharp	% S	Sharp-Rounded	% S-R	Rounded-Sharp	% R-S	Rounded	% R	Rounded-Blunt	% R-B	Blunt-Rounded	% B-R	Blunt	% B
SK M4	3	0	**0**	1	**33**	1	**33**	0	**0**	1	**33**	0	**0**	0	**0**
SK M5	21	1	**5**	5	**24**	5	**24**	4	**19**	4	**19**	1	**5**	1	**4.76**
SK M5 E	2	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
SK M5 W	8	1	**13**	2	**25**	0	**0**	2	**25**	0	**0**	3	**38**	0	**0**
SKX M1	6	1	**17**	3	**50**	1	**17**	0	**0**	0	**0**	1	**17**	0	**0**
SKX M1 LB	2	0	**0**	2	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
SKX M2	161	7	**4**	44	**27**	23	**14**	22	**14**	13	**8**	29	**18**	23	**14.29**
SKX M3	32	1	**3**	9	**28**	10	**31**	4	**13**	2	**6**	2	**6**	4	**12.50**
GA	2	0	**0**	1	**50**	0	**0**	0	**0**	1	**50**	0	**0**	0	**0**
KA	16	3	**19**	5	**31**	5	**31**	1	**6**	1	**6**	1	**6**	0	**0**
KE/D	1	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
KW	11	1	**9**	6	**55**	0	**0**	0	**0**	3	**27**	1	**9**	0	**0**
PL	17	3	**18**	6	**35**	4	**24**	0	**0**	3	**18**	0	**0**	1	**5.88**
CoH	4	1	**25**	0	**0**	1	**25**	2	**50**	0	**0**	0	**0**	0	**0**
SK PM6 Infill	1	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
SK unstrat.	2	0	**0**	0	**0**	1	**50**	0	**0**	0	**0**	0	**0**	1	**50**
Modern	105	27	**26**	17	**16**	13	**12**	23	**22**	14	**13**	5	**5**	6	**5.71**

Table 8.24: Mesowear trend through time via Antidorcas Mesowear III scores. Number of individuals with each category and their relevant percentages within the Antidorcas assemblage. Percentages are rounded to 2 decimal places where necessary. SK=Sterkfontein, SKX=Swartkrans, K=Kromdraai, GL=Gladysvale, PL=Plovers Lake, G=Gondolin, CC=Cooper's Cave, CoH=Cave of Hearths, each provenance is listed with its relevant Member number/letter. 'unstrat'=unstratified.

		Mesowear III score							
Provenance	Total N	1	**1%**	2	**2%**	3	**3%**	4	**4%**
SK M4	1	0	**0**	0	**0**	1	**100**	0	**0**
SK M5	17	0	**0**	0	**0**	2	**12**	15	**88.24**
SK M5 E	2	1	**50**	0	**0**	0	**0**	1	**50**
SK M5 W	1	0	**0**	0	**0**	0	**0**	1	**100**
SKX M1	4	0	**0**	0	**0**	3	**75**	1	**25**
SKX M1 LB	2	0	**0**	0	**0**	2	**100**	0	**0**
SKX M2	12	1	**8**	3	**25**	4	**33**	4	**33.33**
SKX M3	25	0	**0**	4	**16**	12	**48**	9	**36**
GA	1	0	**0**	1	**100**	0	**0**	0	**0**
KA	16	1	**6**	7	**44**	6	**38**	2	**12.5**
KE/D	1	0	**0**	0	**0**	1	**100**	0	**0**
KW	6	1	**17**	1	**17**	3	**50**	1	**16.67**
PL	17	0	**0**	1	**6**	3	**18**	13	**76.47**
CoH	4	0	**0**	0	**0**	2	**50**	2	**50**
SK unstrat.	2	0	**0**	0	**0**	0	**0**	2	**100**
Modern	19	6	**32**	6	**32**	6	**32**	1	**5.26**

Mesowear through time (Member), separated by species for maxillary molars

Only Members where mesowear measurements were taken are shown in each table.

Table 8.25: Antidorcas occlusal relief and cusp shape through time (per Member), with modern A. marsupialis maxillary molars for comparison, shown in number of specimens per category and their respective percentages. Percentages rounded to two decimal places where necessary.

Antidorcas species	Provenance	Total N	High	**% High**	Low	**% Low**	Blunt	**% B**	Rounded	**% R**	Sharp	**%S**
sp.	Sterkfontein Member 5 East	2	0	**0**	2	**100**	0	**0.00**	0	**0.00**	2	**100.00**
	Sterkfontein Member 5 West	3	0	**0**	3	**100**	1	**33.33**	2	**66.67**	0	**0.00**
	Swartkrans Member 1	1	1	**100**	0	**0**	0	**0.00**	1	**100.00**	0	**0.00**
	Swartkrans Member 1 LB	1	1	**100**	0	**0**	0	**0.00**	0	**0.00**	1	**100.00**
	Swartkrans Member 2	114	11	**9.65**	103	**90.35**	38	**33.33**	43	**37.72**	33	**28.95**
	Kromdraai W	1	0	**0**	1	**100**	0	**0.00**	1	**100.00**	0	**0.00**
	Sterkfontein unstratified	2	1	**50**	1	**50**	0	**0.00**	0	**0.00**	2	**100.00**
recki	Sterkfontein Member 4	3	1	**33.33**	2	**66.67**	0	**0.00**	2	**66.67**	1	**33.33**
	Sterkfontein Member 5	6	0	**0.00**	6	**100.00**	1	**16.67**	3	**50.00**	2	**33.33**
	Sterkfontein Member 5 West	3	0	**0.00**	3	**100.00**	1	**33.33**	0	**0.00**	2	**66.67**
	Swartkrans Member 1	3	0	**0.00**	3	**100.00**	1	**33.33**	0	**0.00**	2	**66.67**
	Swartkrans Member 2	14	1	**7.14**	13	**92.86**	9	**64.29**	2	**14.29**	3	**21.43**
	Swartkrans Member 3	12	2	**16.67**	10	**83.33**	5	**41.67**	4	**33.33**	3	**25.00**
	Kromdraai A	13	1	**7.69**	12	**92.31**	0	**0.00**	5	**38.46**	8	**61.54**
	Kromdraai E/D	1	1	**100.00**	0	**0.00**	0	**0.00**	1	**100.00**	0	**0.00**
	Kromdraai W	5	1	**20.00**	4	**80.00**	1	**20.00**	1	**20.00**	3	**60.00**
	Plovers Lake	2	0	**0.00**	2	**100.00**	1	**50.00**	0	**0.00**	1	**50.00**

Antidorcas species	Provenance	Total N	High	**% High**	Low	**% Low**	Blunt	**% B**	Rounded	**% R**	Sharp	**%S**
	Cooper's Cave	1	0	**0.00**	1	**100.00**	0	**0.00**	0	**0.00**	1	**100.00**
bondi	Sterkfontein Member 5	14	1	**7.14**	13	**92.86**	1	**7.14**	10	**71.43**	3	**21.43**
	Sterkfontein Member 5 West	2	0	**0.00**	2	**100.00**	1	**50.00**	0	**0.00**	1	**50.00**
	Swartkrans Member 2	42	8	**19.05**	34	**80.95**	5	**11.90**	21	**50.00**	16	**38.10**
	Swartkrans Member 3	2	2	**100.00**	0	**0.00**	0	**0.00**	1	**50.00**	1	**50.00**
	Kromdraai A	3	0	**0.00**	3	**100.00**	0	**0.00**	3	**100.00**	0	**0.00**
	Plovers Lake	9	0	**0.00**	9	**100.00**	0	**0.00**	3	**33.33**	6	**66.67**
	Cave of Hearths	22	9	**40.91**	13	**59.09**	3	**13.64**	13	**59.09**	6	**27.27**
	Sterkfontein PM6 Infill	1	0	**0.00**	1	**100.00**	0	**0.00**	0	**0.00**	1	**100.00**
	Sterkfontein unstratified	2	0	**0.00**	2	**100.00**	1	**50.00**	1	**50.00**	0	**0.00**
fossil marsupialis	Sterkfontein Member 5	1	0	**0.00**	1	**100.00**	0	**0.00**	0	**0.00**	1	**100.00**
	Swartkrans Member 1	5	1	**20.00**	4	**80.00**	1	**20.00**	1	**20.00**	3	**60.00**
	Swartkrans Member 1 LB	4	3	**75.00**	1	**25.00**	0	**0.00**	0	**0.00**	4	**100.00**
	Swartkrans Member 2	21	5	**23.81**	16	**76.19**	4	**19.05**	5	**23.81**	12	**57.14**
	Swartkrans Member 3	44	26	**59.09**	18	**40.91**	4	**9.09**	21	**47.73**	19	**43.18**
	Gondolin A	2	0	**0.00**	2	**100.00**	0	**0.00**	1	**50.00**	1	**50.00**
	Kromdraai W	5	4	**80.00**	1	**20.00**	0	**0.00**	1	**20.00**	4	**80.00**
	Plovers Lake	6	0	**0.00**	6	**100.00**	1	**16.67**	3	**50.00**	2	**33.33**
	Cave of Hearths	8	4	**50.00**	4	**50.00**	0	**0.00**	3	**37.50**	5	**62.50**
	Modern *Antidorcas marsupialis*	107	53	**49.53**	54	**50.47**	12	**11.21**	50	**46.73**	45	**42.06**

Table 8.26: Antidorcas mesowear scores through time (per Member), with modern A. marsupialis for comparison, shown in number of specimens per category and their respective percentages. Percentages rounded to two decimal places where necessary.

Antidorcas species	Provenance	N Total	LB	**%LB**	LR	**%LR**	LS	**%LS**	HB	**%HB**	HR	**% HR**	HS	**% HS**
sp.	Sterkfontein Member 5 East	2	0	**0**	0	**0**	2	**100**	0	**0**	0	**0**	0	**0**
	Sterkfontein Member 5 West	3	1	**33**	2	**67**	0	**0**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 1	1	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**
	Swartkrans Member 1 LB	1	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**
	Swartkrans Member 2	114	38	**33**	39	**34**	26	**23**	0	**0**	4	**3.51**	7	**6.14**
	Kromdraai W	1	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	Sterkfontein unstratified	2	0	**0**	0	**0**	1	**50**	0	**0**	0	**0**	1	**50**
recki	Sterkfontein Member 4	3	0	**0**	2	**66.67**	0	**0**	0	**0**	0	**0**	1	**33.33**
	Sterkfontein Member 5	6	1	**16.67**	3	**50**	2	**33.33**	0	**0**	0	**0**	0	**0**
	Sterkfontein Member 5 West	3	1	**33.33**	0	**0**	2	**66.67**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 1	3	1	**33.33**	0	**0**	2	**66.67**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 2	14	9	**64.29**	1	**7.14**	3	**21.43**	0	**0**	1	**7.14**	0	**0**
	Swartkrans Member 3	12	5	**41.67**	3	**25**	2	**16.67**	0	**0**	1	**8.33**	1	**8.33**
	Kromdraai A	13	0	**0**	5	**38.46**	7	**53.85**	0	**0**	0	**0**	1	**7.69**
	Kromdraai E/D	1	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**
	Kromdraai W	5	1	**20**	1	**20**	2	**40**	0	**0**	0	**0**	1	**20**
	Plovers Lake	2	1	**50**	0	**0**	1	**50**	0	**0**	0	**0**	0	**0**
	Cooper's Cave	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**

Antidorcas species	Provenance	N Total	LB	**%LB**	LR	**%LR**	LS	**%LS**	HB	**%HB**	HR	**% HR**	HS	**% HS**
bondi	Sterkfontein Member 5	14	1	**7.14**	9	**64.29**	3	**21.43**	0	**0**	1	**7.14**	0	**0**
	Sterkfontein Member 5 West	2	1	**50**	0	**0**	1	**50**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 2	42	5	**11.90**	14	**33.33**	15	**35.71**	0	**0**	7	**16.67**	1	**2.38**
	Swartkrans Member 3	2	0	**0**	0	**0**	0	**0**	0	**0**	1	**50**	1	**50**
	Kromdraai A	3	0	**0**	3	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	Plovers Lake	9	0	**0**	3	**33.33**	6	**66.67**	0	**0**	0	**0**	0	**0**
	Cave of Hearths	22	3	**13.64**	7	**31.82**	3	**13.64**	0	**0**	6	**27.27**	3	**13.64**
	Sterkfontein PM6 Infill	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
	Sterkfontein unstratified	2	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**	0	**0**
	Provenance	N Total	LB	**%LB**	LR	**%LR**	LS	**%LS**	HB	**%HB**	HR	**% HR**	HS	**% HS**
	Sterkfontein Member 5	14	1	**7.14**	9	**64.29**	3	**21.43**	0	**0**	1	**7.14**	0	**0**
	Sterkfontein Member 5 West	2	1	**50**	0	**0**	1	**50**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 2	42	5	**11.90**	14	**33.33**	15	**35.71**	0	**0**	7	**16.67**	1	**2.38**
	Swartkrans Member 3	2	0	**0**	0	**0**	0	**0**	0	**0**	1	**50**	1	**50**
	Kromdraai A	3	0	**0**	3	**100**	0	**0**	0	**0**	0	**0**	0	**0**
	Plovers Lake	9	0	**0**	3	**33.33**	6	**66.67**	0	**0**	0	**0**	0	**0**
	Cave of Hearths	22	3	**13.64**	7	**31.82**	3	**13.64**	0	**0**	6	**27.27**	3	**13.64**
	Sterkfontein PM6 Infill	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
	Sterkfontein unstratified	2	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**	0	**0**

Antidorcas species	Provenance	N Total	LB	**%LB**	LR	**%LR**	LS	**%LS**	HB	**%HB**	HR	**% HR**	HS	**% HS**
fossil marsupialis	Sterkfontein Member 5	1	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 1	5	1	**20**	1	**20**	2	**40**	0	**0**	0	**0**	1	**20**
	Swartkrans Member 1 LB	4	0	**0**	0	**0**	1	**25**	0	**0**	0	**0**	3	**75**
	Swartkrans Member 2	21	4	**19.05**	4	**19.05**	8	**38.10**	0	**0**	1	**4.76**	4	**19.05**
	Swartkrans Member 3	44	4	**9.09**	12	**27.27**	2	**4.55**	0	**0**	9	**20.45**	17	**38.64**
	Gondolin A	2	0	**0**	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**
	Kromdraai W	5	0	**0**	1	**20**	0	**0**	0	**0**	0	**0**	4	**80**
	Plovers Lake	6	1	**16.67**	3	**50**	2	**33.33**	0	**0**	0	**0**	0	**0**
	Cave of Hearths	8	0	**0**	2	**25**	2	**25**	0	**0**	1	**12.50**	3	**37.50**
Modern *Antidorcas marsupialis*		107	10	**9.35**	31	**28.97**	13	**12.15**	2	**1.87**	19	**17.76**	32	**29.91**

Table 8.27: Antidorcas sp. new occlusal relief categories through time (per Member),with modern A. marsupialis for comparison, shown in number of specimens per category and their respective percentages. Percentages rounded to two decimal places where necessary.

Antidorcas species	Provenance	Total N	High	**% High**	Medium	**% Medium**	Low	**% Low**
sp.	Sterkfontein Member 5 East	2	0	**0**	0	**0**	2	**100**
	Sterkfontein Member 5 West	3	0	**0**	1	**33**	2	**66.67**
	Swartkrans Member 2	91	0	**0**	17	**19**	74	**81.32**
	Kromdraai W	1	0	**0**	1	**100**	0	**0**
recki	Sterkfontein Member 4	3	0	**0**	1	**33.33**	2	**66.67**
	Sterkfontein Member 5	6	0	**0**	0	**0**	6	**100**
	Sterkfontein Member 5 West	3	1	**33.33**	0	**0**	2	**66.67**

Antidorcas species	Provenance	Total N	High	**% High**	Medium	**% Medium**	Low	**% Low**
	Swartkrans Member 1	3	0	**0**	1	**33.33**	2	**66.67**
	Swartkrans Member 2	14	0	**0**	5	**35.71**	9	**64.29**
	Swartkrans Member 3	12	2	**16.67**	2	**16.67**	8	**66.67**
	Kromdraai A	13	0	**0**	2	**15.38**	11	**84.62**
	Kromdraai E/D	1	0	**0**	1	**100**	0	**0**
	Kromdraai W	5	0	**0**	2	**40**	3	**60**
	Plovers Lake	2	0	**0**	0	**0**	2	**100**
bondi	Sterkfontein Member 5	14	0	**0**	5	**35.71**	9	**64.29**
	Sterkfontein Member 5 West	2	0	**0**	1	**50**	1	**50**
	Swartkrans Member 2	37	1	**2.70**	8	**21.62**	28	**75.68**
	Swartkrans Member 3	2	2	**100**	0	**0**	0	**0**
	Kromdraai A	3	0	**0**	2	**66.67**	1	**33.33**
	Plovers Lake	9	0	**0**	2	**22.22**	7	**77.78**
	Cave of Hearths	1	0	**0**	1	**100**	0	**0**
	Sterkfontein PM6 Infill	1	0	**0**	0	**0**	1	**100**
	Sterkfontein unstratified	2	0	**0**	0	**0**	2	**100**
fossil marsupialis	Sterkfontein Member 5	1	0	**0**	0	**0**	1	**100**
	Swartkrans Member 1	3	0	**0**	2	**66.67**	1	**33.33**
	Swartkrans Member 1 LB	2	0	**0**	1	**50**	1	**50**
	Swartkrans Member 2	19	3	**15.79**	2	**10.53**	14	**73.68**

Antidorcas species	Provenance	Total N	High	**% High**	Medium	**% Medium**	Low	**% Low**
	Swartkrans Member 3	18	2	**11.11**	8	**44.44**	8	**44.44**
	Gondolin A	2	0	**0**	0	**0**	2	**100**
	Kromdraai W	5	4	**80**	0	**0**	1	**20**
	Plovers Lake	6	0	**0**	1	**16.67**	5	**83.33**
	Cave of Hearths	3	0	**0**	1	**33.33**	2	**66.67**
Modern *Antidorcas marsupialis*		105	30	**28.57**	54	**51.43**	21	**20.00**

Table 8.28: Antidorcas sp. new occlusal cusp shape categories through time (per Member), with modern A. marsupialis for comparison, shown in number of specimens per category and their respective percentages. Percentages rounded to two decimal places where necessary.

Antidorcas species	Provenance	Total N	Sharp	**% S**	S-R	**% S-R**	R-S	**% R-S**	Rounded	**% R**	R-B	**%R-B**	B-R	**%B-R**	Blunt	**%B**
sp.	Sterkfontein Member 5 East	2	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
	Sterkfontein Member 5 West	3	0	**0**	0	**0**	0	**0**	2	**66.67**	0	**0**	1	**33.33**	0	**0**
	Swartkrans Member 2	91	3	**3.30**	21	**23.08**	17	**18.68**	12	**13.19**	5	**5.49**	19	**20.88**	14	**15.38**
	Kromdraai W	1	0	**0**	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**
recki	Sterkfontein Member 4	3	0	**0**	1	**33.33**	1	**33.33**	0	**0**	1	**33.33**	0	**0**	0	**0**
	Sterkfontein Member 5	6	0	**0**	2	**33.33**	0	**0**	0	**0**	3	**50**	1	**16.67**	0	**0**
	Sterkfontein Member 5 West	3	1	**33.33**	1	**33.33**	0	**0**	0	**0**	0	**0**	1	**33.33**	0	**0**
	Swartkrans Member 1	3	0	**0**	2	**66.67**	0	**0**	0	**0**	0	**0**	1	**33.33**	0	**0**

Antidorcas species	Provenance	Total N	Sharp	**% S**	S-R	**% S-R**	R-S	**% R-S**	Rounded	**% R**	R-B	**%R-B**	B-R	**%B-R**	Blunt	**%B**
	Swartkrans Member 2	14	0	**0**	2	**14.29**	1	**7.14**	2	**14.29**	0	**0**	4	**28.57**	5	**35.71**
	Swartkrans Member 3	12	0	**0**	3	**25**	3	**25**	1	**8.33**	0	**0**	2	**16.67**	3	**25**
	Kromdraai A	13	3	**23.08**	5	**38.46**	3	**23.08**	0	**0**	1	**7.69**	1	**7.69**	0	**0**
	Kromdraai E/D	1	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
	Kromdraai W	5	0	**0**	3	**60**	0	**0**	0	**0**	1	**20**	1	**20**	0	**0**
	Plovers Lake	2	1	**50**	0	**0**	0	**0**	0	**0**	1	**50**	0	**0**	0	**0**
bondi	Sterkfontein Member 5	14	0	**0**	3	**21.43**	5	**35.71**	4	**28.57**	1	**7.14**	0	**0**	1	**7.14**
	Sterkfontein Member 5 West	2	0	**0**	1	**50**	0	**0**	0	**0**	0	**0**	1	**50**	0	**0**
	Swartkrans Member 2	37	3	**8.11**	12	**32.43**	3	**8.11**	6	**16.22**	7	**18.92**	4	**10.81**	2	**5.41**
	Swartkrans Member 3	2	0	**0**	1	**50**	1	**50**	0	**0**	0	**0**	0	**0**	0	**0**
	Kromdraai A	3	0	**0**	0	**0**	2	**66.67**	1	**33.33**	0	**0**	0	**0**	0	**0**
	Plovers Lake	9	1	**11.11**	5	**55.56**	3	**33.33**	0	**0**	0	**0**	0	**0**	0	**0**
	Cave of Hearths	1	0	**0**	0	**0**	0	**0**	1	**100**	0	**0**	0	**0**	0	**0**
	Sterkfontein PM6 Infill	1	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
	Sterkfontein unstratified	2	0	**0**	0	**0**	1	**50**	0	**0**	0	**0**	0	**0**	1	**50**
fossil marsupialis	Sterkfontein Member 5	1	1	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**

Antidorcas species	Provenance	Total N	Sharp	**% S**	S-R	**% S-R**	R-S	**% R-S**	Rounded	**% R**	R-B	**%R-B**	B-R	**%B-R**	Blunt	**%B**
	Swartkrans Member 1	3	1	**33.33**	1	**33.33**	1	**33.33**	0	**0**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 1 LB	2	0	**0**	2	**100**	0	**0**	0	**0**	0	**0**	0	**0**	0	**0**
	Swartkrans Member 2	19	1	**5.26**	9	**47.37**	2	**10.53**	2	**10.53**	1	**5.26**	2	**10.53**	2	**10.53**
	Swartkrans Member 3	18	1	**5.56**	5	**27.78**	6	**33.33**	3	**16.67**	2	**11.11**	0	**0**	1	**5.56**
	Gondolin A	2	0	**0**	1	**50**	0	**0**	0	**0**	1	**50**	0	**0**	0	**0**
	Kromdraai W	5	1	**20**	3	**60**	0	**0**	0	**0**	1	**20**	0	**0**	0	**0**
	Plovers Lake	6	1	**16.67**	1	**16.67**	1	**16.67**	0	**0**	2	**33.33**	0	**0**	1	**16.67**
	Cave of Hearths	3	1	**33.33**	0	**0**	1	**33.33**	1	**33.33**	0	**0**	0	**0**	0	**0**
Modern *Antidorcas marsupialis*		105	27	**25.71**	17	**16.19**	13	**12.38**	23	**21.90**	14	**13.33**	5	**4.76**	6	**5.71**

8.3 STATISTICAL ANALYSIS

By using a continuous scale variable (new mesowear score), a greater number of statistical tests are compatible. Pairwise comparisons of *Antidorcas* as a genus for each provenance were conducted (Table 8.29) and for each *Antidorcas* species, to consider their relative palaeoecology, were created (Table 8.30). *Antidorcas*, as a genus, showed significant differences in new mesowear scores through time (across provenance) [maxillary molars (N=394): p<.000; mandibular molars (N=249): p<.000].

Sterkfontein Member 5 and Modern *Antidorcas* are the only provenances consistently significantly different in new mesowear scores for maxillary and mandibular dentition. Sterkfontein Member 5 West and modern; Kromdraai W and Swartkrans Member 2 show difference via LSD (less conservative) post-hoc tests for both maxillary and mandibular dentition (Table 8.29).

A. recki and *A. marsupialis* showed no significant differences in new mesowear score through time (via non-parametric independent samples kruskal-wallis analysis or parametric ANOVAs) so were not subject to post-hoc analyses.

Maxillary new mesowear scores differ significantly through time (across provenance) p=.035 for *A. bondi.* Mandibular new mesowear scores also differ significantly through time (across provenance) p=.013 for *A. bondi. A. bondi* pairwise comparisons are detailed in Table 8.30.

Table 8.29: Pairwise comparison of provenance for Antidorcas as a genus, for mesowear (new mesowear score), showing where significant differences between provenance exists. Values above the line are from the more conservative, Tukey's HSD post-hoc test, and those below the lines from the less conservative, LSD post-hoc test (with associated p values, significance level p=.05); maxillary molars are represented by bold text and mandibular in normal text.

	SK M4	KW	SK M5	SK M5E	SK M5W	SKX M1	SKX M1 LB	SKX M1 HR	KA	GD	SKX M2	CC	SKX M3	SK LC	SK PM6	PL	COH	GV	MDN
SK M4																			
KW																			p=.031
SK M5	p=.023	**p=.032**																	**p=.007;** p=.038
SK M5E	p=.046																		
SK M5W		p=.026																	
SKX M1		p=.025																	
SKX M1 LB																			
SKX M1 HR																			
KA		p=.005																	
GD																			
SKX M2		**p=.004;** p=.001	p=.013		p=.004														**p<.000**
CC																			
SKX M3		p=.003									**p=.002**								
SK LC																			
SK PM6	p=.049																		
PL		p=.019																	
COH																			
GV																			
MDN		p<.000	**p<.000;** p<.000	p=.017	**p=.003;** p=.006						**p<.000**		**p=.017**		p=.043	**p<.000**	p=.036		

Table 8.30: Pairwise comparison of provenance for Antidorcas bondi, for mesowear (new mesowear score), showing where significant differences between provenance exists. Values in bold above the line are from the more conservative, Tukey's HSD post-hoc test, and those below the lines from the less conservative, LSD post-hoc test (with associated p values, significance level p=.05); maxillary molars are represented by bold text and mandibular in normal text.

	SK M4	KW	SK M5	SK M5E	SK M5W	SKX M1	SKX M1 LB	SKX M1 HR	KA	GD	SKX M2	CC	SKX M3	SK LC	SK PM6	PL	COH	GV
SK M4		**p=.028**																
KW	**p<.000**																	
SK M5		**p=.014**									p=.006							
SK M5E																		
SK M5W	**p=.007**																	
SKX M1	**p=.038**		p=.023		p=.043													
SKX M1 LB	**p=.043**																	
SKX M1 HR																		
KA		**p=.002**			**p=.022**													
GD																		
SKX M2		**p=.036**																
CC																		
SKX M3	**p=.040**	**p=.038**																
SK LC						p=.030					p=.032							
SK PM6																		
PL						p=.042					p=.005							
COH																		
GV																		

8.3.1. Data reduction

A principal component analysis was run on mesowear variables for all *Antidorcas* species' upper second molars, from all provenances to reduce the number of variables. Mesowear score (0-4 and 1-6) were too closely correlated (shown via a Pearson's correlation) and were removed from this factor analysis. The data taken forward were middling (KMO=0.708) and were appropriate to use in a factor reduction (p=.000) (Table 8.31-Table 8.32; Figure 8.1).

Table 8.31: PCA results for Antidorcas UM2 Mesowear variables. KMO and Bartlett's Test to show data is suitable for factor analysis (see blue boxes).

A) KMO and Bartlett's Test

Kaiser-Meyer-Olkin Measure of Sampling Adequacy		.708
Bartlett's Test of Sphericity	Approx. Chi-Square	483.878
	df	15
	significance	.000

B) Communalities

	Initial	Extraction
Relief	1.000	.808
Cusp Shape	1.000	.923
New Mesowear Score	1.000	.946
New Relief	1.000	.873
New Cusp Shape	1.000	.917
Mesowear III	1.000	.599

Extraction Method: Principal Component Analysis.

C) Total Variance

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings			Rotation Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	3.844	64.072	64.072	3.844	64.072	64.072	3.079	51.311	51.311
2	1.223	20.378	84.450	1.223	20.378	84.450	1.988	33.140	84.450
3	.499	8.312	92.762						
4	.253	4.216	96.978						
5	.140	2.339	99.317						
6	.041	.683	100.000						

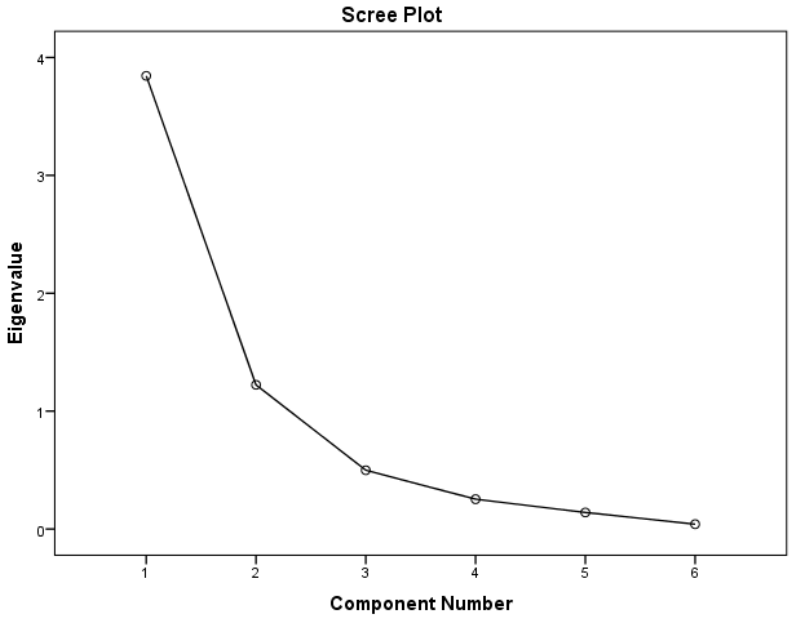


Figure 8.1: PCA scree plot for Antidorcas UM2 Mesowear variables.

Table 8.32: PCA results for Antidorcas UM2 mesowear variables: A) component matrix Extraction Method: Principal component analysis. 2 components extracted. B) rotated component matrix copied from SPSS output to show loadings of each variable on the relevant component. Rotation Method: Varimax with Kaiser normalisation. Rotation converged in 3 iterations.

A) Component Matrix

	Component	
	1	2
Relief	.786	
Cusp shape	-.643	.713
New mesowear score	-.937	
New relief	.892	
New cusp shape	.740	-.607
Mesowear III	.768	

B) Rotated Component Matrix

	Component	
	1	2
Relief	.897	
Cusp shape		-.948
New mesowear score	-.929	
New relief	.901	
New cusp shape		.911
Mesowear III	.698	

Cusp shape, regardless of number of discrete categories, separates out from the other mesowear variables. The other mesowear variables account for the majority of the variation seen in the dataset, grouping on the principal component, and therefore, would appear better dietary indicators. From the principal component analysis, two components can be used in the multi-method analysis. 'Mesowear score' as component 1, (new mesowear

score, relief and new relief and mesowear III) and 'cusp shape' as component 2 (cusp shape).

Discriminant Function Analysis (DFA):

The DFA for upper second molars according to provenance predictor model has 44.4% accuracy, suggesting *Antidorcas* lifetime diet (as evidenced by mesowear) **cannot** be accurately predicted according to provenance. No obvious clusters emerge to indicate mesowear (dietary/palaeovegetation) change through time (see Appendix A7). Mesowear score 1-6 was not an accurate enough predictor variable and was removed from the analysis. As this DFA could not be used to answer the central research questions, the results of the DFA are not included here but can be found in Appendix A7.

8.3.2 Mesowear III by Species:

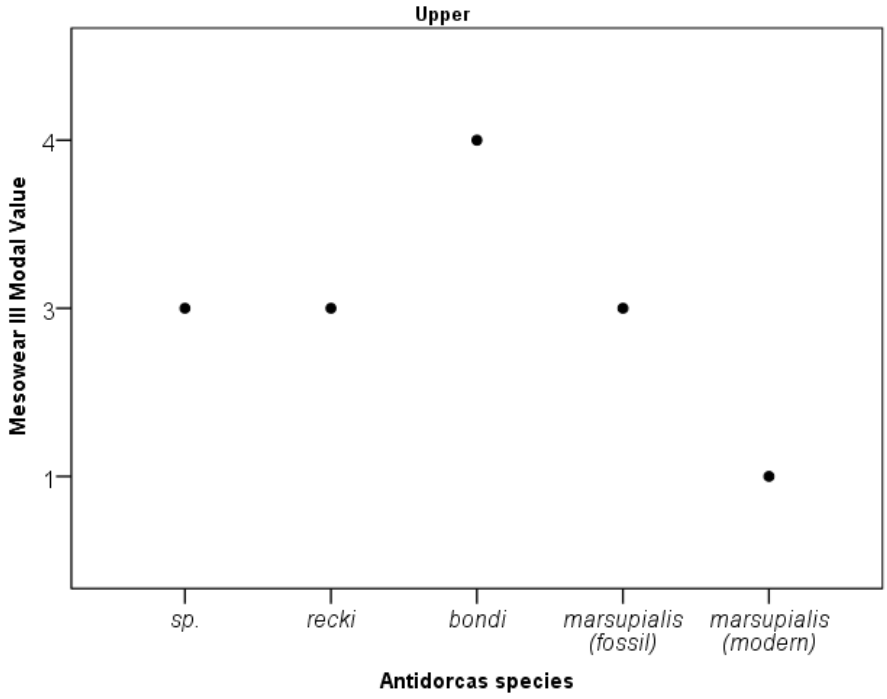


Figure 8.2: Scatter plot showing the modal Mesowear III score given according to species. Mesowear III is applied to the second upper molar. No species yielded an average score of '2' therefore, this score was removed from this plot.

Based on this *Antidorcas* dataset, Mesowear III shows promise as a palaeodietary indicator (Figure 8.2). *A. bondi* displays a distinct grazing signal. Contrastingly, the modern springbok shows a browsing signal. Larger sample sizes would be beneficial to extrapolate more from this method.

8.3.3 Statistical Analysis Explanation

Kruskal-Wallis and post-hoc Mann-Whitney U pairwise comparison tests with Bonferroni adjustment were carried out for all mesowear variables for all *Antidorcas* species combined to assess differences between members; and for all members combined to assess species differences for *Antidorcas* and for each *Antidorcas* species within each member.

Maxillary dentition showed significant differences across *Antidorcas* species for Swartkrans Member 2 between *A. recki* (n=14) and *A. bondi* (n=42) for cusp shape (p=0.005) and between *Antidorcas* sp. (n=114) and *A. bondi* (p=0.003) and *A. recki* and *A. bondi* (p=0.005) for mesowear scores (scale 1-6).

The variation shown by the different *Antidorcas* species within Swartkrans Member 2 is interesting. This member has larger sample sizes and could have encapsulated the range of variation representative of living populations. This could only be shown by comparisons with similar size datasets, where available. *A. bondi* tends towards rounded cusps and low relief, as may be expected, albeit with higher numbers of sharp cusps and lower of blunt cusps than may be expected of a catholic grazer. Surprisingly, *A. recki* has very low incidence of sharp cusps and often shows blunt cusps (64%) and consistently low relief (LB 33%, LR 34%, LS 23%). Swartkrans Member 2 has been shown by others (e.g. Steininger 2012) to be against the increased grassland trend, with a higher incidence of browsing signals. This is not the case from the *Antidorcas* dataset here, which shows a more abrasive diet for Swartkrans Member 2 (a dominance of low relief and rounded to blunt cusps) and may be indicative of the palaeoecology of *Antidorcas* of the time or likely of habitat heterogeneity for Swartkrans Member 2 (c.1.7-1.07 Ma).

Mandibular dentition showed significant differences for mesowear scores (scale 1-6) for *A. bondi* between Sterkfontein Member 5 (n=12) and Cave of Hearths (n=20) ($p<0.0005$). *A. bondi* in Sterkfontein Member 5 has more occurrences of lower relief and blunt cusps, and is dominated by low relief, rounded cusps (58%). Conversely, Cave of Hearths has consistently higher relief and sharper cusps (0% low, blunt; low sharp 25%, high, rounded 35% and high, sharp 35%). This suggests that *A. bondi* was eating more browse at Cave of Hearths than earlier, in Sterkfontein Member 5. Cave of Hearths is close to the LAD for the species and the change in diet could suggest nutritional stress leading to their demise, yet this cannot be proven with mesowear and this dataset alone. Cave of Hearths is also geographically separated from the Sterkfontein valley and could simply represent a local population.

Fossil specimens were analysed, testing for differences in mesowear variables as outlined above, across species, provenance (site and member-assemblage) and per species within each provenance. Basic descriptive statistics were calculated, followed by testing for significant differences with Independent samples Kruskal-Wallis tests and relevant post-hoc tests (Table 8.29 and Table 8.30).

There were no significant differences across genera for mesowear values when using the 0-4 scoring system (Louys et al. 2012; Kaiser et al. 2009). As differences in wear patterns would be expected between genera with differing diets, the mesowear scoring system of 1-6 values was taken forward to be used for further analysis in this research. No significant difference across genera for the mesowear III method (Solounias et al. 2014) was found. Yet the basic descriptive statistics had appeared to establish dietary categories as might be expected (i.e. *A. recki* as a browser and *A. bondi* and *D.pygragus* as grazers) based on the mesowear III (or inner mesowear) scores. Mesowear III scores totalled a small sample size, particularly for supplementary species so any patterns may simply not emerge under statistical scrutiny.

8.4 DISCUSSION

Following protocol established by Fortelius and Solounias (2000), mesowear was conducted on fossil *Antidorcas*. Limitations to this method quickly became apparent and further categories were included to tailor the method to these particular research questions posed here and ensure that the range of variation typical of mixed-feeding herbivores was captured.

Should mixed feeders/*Antidorcas* have more discrete mesowear categories to better understand their dietary signal?

A recent experiment found that at least 6 months is required to impart a mesowear signal on dentition (Ackermans et al. 2018). This may explain why mixed feeders do not tend to provide any one typical mesowear category (but a range that are not reflective of either habitual grazing or habitual browsing diets), this would be especially pertinent of mixed feeding of individuals on a seasonal scale.

'Medium relief' tends to take away more often from the high relief category (reducing the browsing element) but not exclusively, suggesting it is a worthwhile addition for mixed feeding antelopes to capture the maximum amount of variation. Additional cusp shape categories show greater distinction between species, for example, *Antidorcas recki* has no specimens with blunt cusps. In contrast, *Antidorcas bondi* has substantially fewer specimens with sharp cusps (Table 8.17, Table 8.18 and Table 8.27) and, more surprisingly, fewer with blunt cusps, in favour of rounded-blunt cusps when additional categories are available. The addition of more mesowear categories thereby increases the distinction in the dietary preferences of these fossil *Antidorcas* species but also perhaps shows *Antidorcas bondi* have a less graze/abrasion-dominated diet than may be anticipated (e.g. Brink and Lee-Thorp 1992). Currently, rounded cusps are implied to be a result of less abrasive diets than complete blunting of cusps. The distinction between the causes of rounded or blunted cusps may require further clarity to extrapolate the grazing/ abrasion ratios acting on *Antidorcas*. A scale of 1-49 LB (low blunt) to HS (high sharp) creates false distinctions and hides mesowear patterns and is extremely time consuming to process so is not a practical application to a method that is known for being relatively quick and simple. The results from this method are given in appendices (Appendix A7).

One of the main mesowear variables, cusp shape, was not a good predictor of diet within *Antidorcas* (see DFA).

Increasing and adjusting the number of variables and categories therefore, for mesowear analysis appears fruitful by allowing a greater degree of differential dietary separation. On balance, the most effective method to achieve a balance between simplicity of use as well as gaining sufficient distinction of dietary preferences, is to include a 'medium' relief category for mixed-feeding herbivores, alongside the traditional 'high' and 'low' categories.

Reflecting on mesowear as a method

Mesowear reflects the cumulative effects of items masticated on throughout the lifetime, both food items (vegetation) and exogenous particles (dust and grit), on the dental

morphology of the animal as a direct indicator of diet and abrasion (Fortelius and Solounias 2000; Semprebon and Rivals 2010). As mesowear variables give a generalised lifetime signal and are impacted by numerous factors, substantially large sample sizes are required to say anything of note. The sample sizes obtained in this research meet these requirements but at other sites, with substantial taphonomic impact and the like, this may not always be possible.

Mixed-feeding species are not as readily differentiated from obligate grazers / browsers or between seasonal / lifetime mixed feeders, based on mesowear variables (e.g. Janis 1995). It became apparent early on in this research that the typical mesowear variables used for this type of study were over simplified and that additional categories may be beneficial. It is possible that the consumption of succulents that could utilise the CAM pathway add another element to this. The phytolith content of these plants, and therefore the baseline abrasiveness, is little studied. Combining the results from this mesowear study with those from the other methods implemented here will shed light on whether the mesowear patterns seen are more reflective of a grazing, or of an alternative, abrasive element.

Taylor et al. (2013), for instance, when *Rhinoceros unicornis* displayed higher attrition-dominated mesowear patterns than anticipated, considering its grazing diet, inferred a low intake of environmental abrasives. Furthermore, they suggested heterogeneous cusps across the toothrow could be reflective of heterogeneous browse, whilst more uniform mesowear across the toothrow would reflect physically more homogeneous vegetation, (inclusive of browse vegetation). *Antidorcas* species showed more homogenous wear patterns than might be anticipated given their differential anticipated diets for species. Unfortunately, here most of the specimens considered for mesowear were isolated molars, so little comparison of homogeneity *across the toothrow* was possible.

Similarly, the differential mesowear signals from upper and lower dentition can confuse the palaeovegetation signal. An example of this is Swartkrans Member 1 lower bank (see Table 8.33), in which *Antidorcas* upper molars yield a strong browsing signal (80% high relief, 100% sharp cusps), which is contrasted by the lower molars, yielding a mixed-feeding, tending towards grazing/ high abrasion (71% low relief, 71% rounded cusps).

Low relief has unexpectedly been found to increase along with an increase in C_4 vegetation in the diet elsewhere due to frugivory (Louys et al. 2012). Here, perhaps frugivory, or similar confounding factors (e.g. feeding on succulents during water scarce times, as practised by the modern springbok) could be impacting on mesowear variables. This would help to explain mesowear variables that are not readily explained by strictly grass versus browse categorical parameters, and aid in the understanding of why greater proportions of low relief arise than may be expected. Alternatively, low relief could be an artefact of the subjectivity of the method being implemented visually. The relatively small dentition of *Antidorcas* can tend towards favouring a 'low relief' assessment, compared to the substantially larger overall dentition of *Tragelaphus strepsiceros* for example. Occlusal relief can be calculated via the measurements taken in this study to reduce subjectivity, dividing occlusal height by occlusal length (Louys et al. 2011). However, this was not

implemented here due to the inconsistency in the completeness of the specimens (often eliminating one or other of the accurate measurements but a relative mesowear score remained achievable visually).

Mesowear has been used as a palaeoenvironmental indicator for aridity (e.g. temperature and precipitation (Kasier and Schulz 2006; Kaiser et al. 2013; Kubo and Yamada 2014)) and vegetation cover. Yet, most found mesowear to be most efficient in showcasing dietary behaviour but unrelated to aridity levels (DeSantis et al. 2018).

Finally, Table 8.34 highlights an issue with the mesowear methodology. Obligate grazers are said to have an abrasion dominated diet, opposed by browsers who have an attrition-dominated diet (Fortelius and Solounias 2000). Yet from this research, it would seem that this method requires further refinement. The categorical placement of grazing-abrasion and browsing-attrition appears a little too simplistic, particularly when considering fossil taxa. Figure 8.3 shows the dentition of a modern grazer, *Damaliscus pygargus*. Whilst an abrasive diet is evident based on the low relief and rounded- blunt cusps apparent on the dentition here, there is also obviously an influence of tooth-on tooth contact, i.e. attrition. Image A shows extreme attrition causing high relief for the maxillary third molar. If found as an isolated molar in a fossil assemblage, the 'sharpest' cusp might score this individual as having high relief, with rounded cusps.

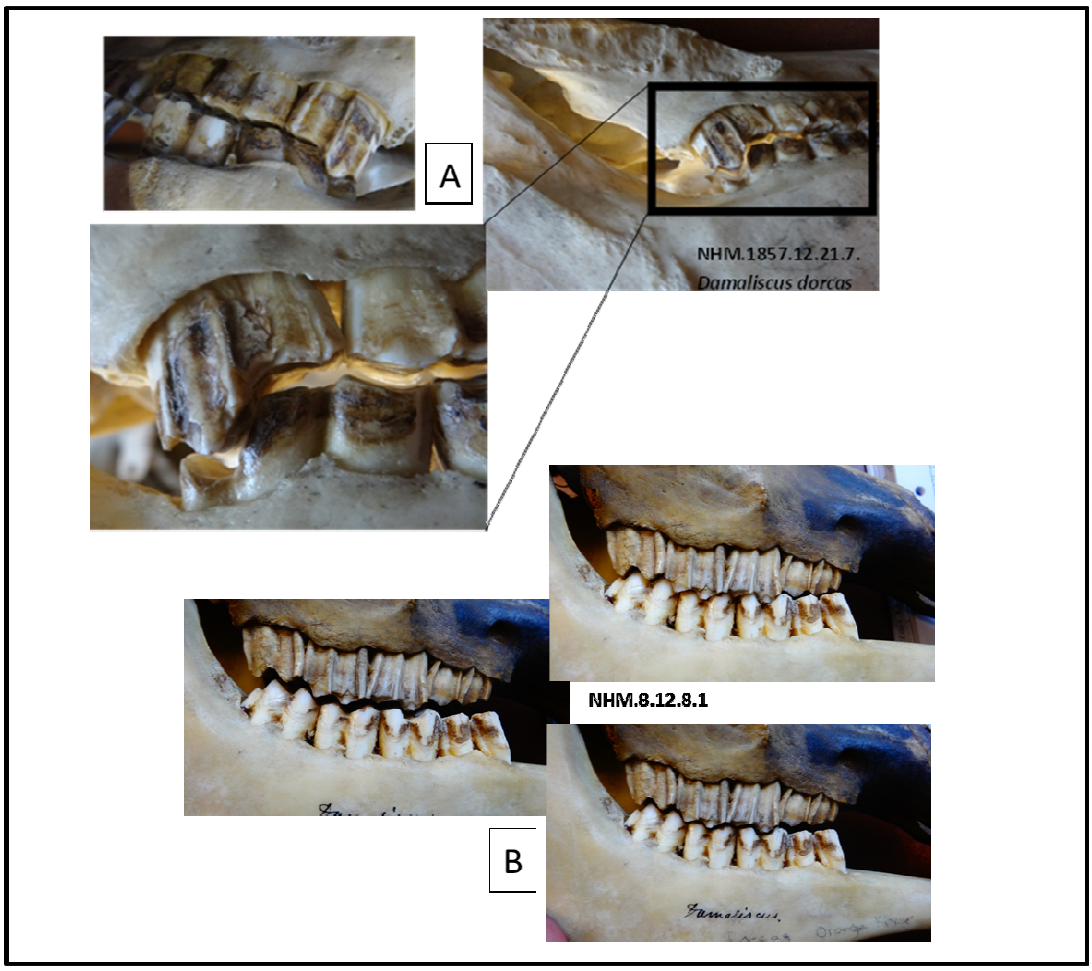


Figure 8.3: Modern Damaliscus pygargus mesowear to show the combined influence of abrasion and attrition despite being an obligate grazer. Image A: NHM 1857.12.21.7, Image B: NHM.8.12.1.

It is suggested that the mesowear method requires more parameters beyond those of occlusal relief and cusp shape to untangle the subtleties of fossil palaeodietary ecologies enabling more accurate palaeoenvironmental reconstructions. Parameters may include factors such as relative cusp height and shape between cusps on the same tooth and along the toothrow.

8.4.1 *Antidorcas* Dietary Palaeoecology

Antidorcas is also separated to species level to extrapolate clearer dietary versus palaeoenvironmental signals, i.e. to ensure that any dietary signal is not averaged or skewed by combining a grazing species and a browsing species.

Interestingly, *A. recki* and *A. bondi* maxillary dentition show no significant differences for any mesowear variable (Kruskal-Wallis independent samples test followed by post-hoc Mann-Whitney U pairwise tests) other than Mesowear III (p=0.001). *A. recki* (n=37) has a significantly lower mean rank than *A. bondi* (n=29). No *A. bondi* specimens displayed a score of 1 (representative of a typical browser) (Solounias et al. 2014). *A. bondi*'s modal score of 4 is typical of a grazing species.

All individual species had significantly different mesowear variables, when compared to *Antidorcas* sp. (*Antidorcas* individuals only identifiable to genus level) *Antidorcas* 'sp.' could represent one species, or a combination of any *Antidorcas* species and is viewed as a mixed *Antidorcas* genus signal. This perhaps suggests that more significant differences

emerge when many species are combined, due to averaging of the grazing, browsing and mixed-feeding groups.

Mesowear signal for each species -*Antidorcas* lineage paleoecology summary

Mesowear III (Solounias et al. 2014) was the most reliable indicator of species dietary preferences, with *A. recki* consistently scoring in line with typical browsing and *A. bondi* consistently scoring in line with typical grazers. *A. marsupialis* mesowear scores align with mixed-feeding diets.

From traditional mesowear scoring systems, (See Table 8.3 and Table 8.15), the following dietary categories prevailed for each species. *A. recki* was mixed-feeding to browsing (low relief, sharp cusps dominate); *A. bondi* was grazing to mixed-feeding (low relief, rounded cusps dominate); Fossil *A. marsupialis* was mixed-feeding (showing an equal weighting of high and low relief, with sharp cusps dominating for upper molars and rounded cusps dominating for lower molars).

8.4.2 Mesowear signal through time – palaeoenvironment

When taxa are combined, relative proportions of each dietary type (along the grazer-browser spectrum, as indicated by mesowear scores) are indicative of palaeoenvironments (Fortelius and Solounias 2000; Vrba 1975, 1980). By ordering each member chronologically, mesowear is indicative of palaeoenvironmental change through time. No obvious directional (i.e. browse-dominated to graze-dominated) dietary transition is apparent within this temporal range from mesowear results.

Table 8.33: Summary of Antidorcas mesowear trend through time, to indicate the likely palaeoenvironment for each Member. The dominant mesowear type is highlighted in purple with Antidorcas diet predicted based on dominant mesowear attributes. Members are organised in relative chronological order.

Provenance	**Dentition**	**High relief (%)**	**Low Relief (%)**	**Sharp cusps (%)**	**Round cusps (%)**	**Blunt cusps (%)**	***Antidorcas* diet**
Sterkfontein M4	Upper	33	67	33	67	0	G-MF
	Lower	40	60	60	40	0	MF
Kromdraai W	Upper	45	55	64	27	9	MF
	Lower	0	100	0	40	60	G
Kromdraai B	Upper	X	X	X	X	X	X
	Lower	0	100	0	100	0	G-MF
Kromdraai E/D	Upper	**100**	0	0	100	0	B-MF
	Lower	0	100	100	0	0	MF
Sterkfontein M5	Upper	5	95	29	62	10	G-MF
	Lower	14	86	31	52	17	G-MF
Sterkfontein M5E	Upper	0	100	100	0	0	MF
	Lower	17	83	17	50	33	G-MF
Sterkfontein M5W	Upper	0	100	38	25	38	MF*
	Lower	0	100	8	67	25	G-MF
Swartkrans M1	Upper	22	78	56	22	22	MF
	Lower	60	40	20	50	30	B-MF
Swartkrans M1LB	Upper	**80**	20	100	0	0	B
	Lower	29	71	29	71	0	G-MF
Swartkrans M1HR	Upper	X	X	X	X	X	X
	Lower	0	100	33	67	0	G-MF
Kromdraai A	Upper	6	94	50	50	0	MF*
	Lower	11	89	63	32	5	MF
Gondolin A	Upper	0	100	50	50	0	MF*

Provenance	Dentition	High relief (%)	Low Relief (%)	Sharp cusps (%)	Round cusps (%)	Blunt cusps (%)	*Antidorcas* diet
	Lower	X	X	X	X	X	X
Swartkrans M2	Upper	13	87	34	37	29	G-MF
	Lower	43	57	22	63	14	G-MF
Coopers Cave	Upper	0	100	100	0	0	MF
	Lower	57	43	71	14	14	B
Swartkrans M3	Upper	**52**	48	40	45	16	B-MF
	Lower	39	61	24	48	28	G-MF
Sterkfontein LC	Upper	X	X	X	X	X	X
	Lower	0	100	0	0	100	G
Sterkfontein PM6	Upper	0	100	100	0	0	MF
	Lower	0	100	0	0	100	G
Plovers Lake	Upper	0	100	53	35	12	MF
	Lower	15	85	54	31	15	MF
Cave of Hearths	Upper	43	57	37	53	10	G-MF
	Lower	52	48	39	58	3	B-MF
Gladysvale	Upper	X	X	X	X	X	X
	Lower	0	100	0	0	100	G
Modern	Upper	50	50	42	47	11	MF*
	Lower	41	59	25	62	13	G-MF

*Mixed-feeding assemblage diets are apparent, with even mesowear percentages between for a particular variable within the *Antidorcas* assemblage.

Table 8.33 summarises the prevailing trend through time, as predicted via *Antidorcas* dominant mesowear attributes. A mixed-feeding diet dominates throughout this temporal range for *Antidorcas*, with Low relief and sharp cusps or rounded cusps occurring most regularly. Although occasionally differentially recorded on upper and lower dentition, no member shows *Antidorcas* to be consistently (upper and lower dentition) exclusively grazing or browsing.

Low relief dominates for both upper and lower dentition, which could be reflective of an abrasive diet. Sharper cusps are evident for upper molars than for lower molars. It was hypothesised that lower molars tend towards blunting (Kaiser and Fortelius 2003). However, although for the entire duration of geological time (i.e. when combining members), lower molars display blunter cusps, lower molars are not consistently blunter than upper molars in each member, when compared to upper molars.

From these deposits, it is not possible to determine if the upper and lower molars are from the same animal. Therefore, the capacity to assess how mesowear manifests in response to differential dietary influence on uppers versus lowers is beyond the remit of this research.

Yet it is possible to speculate on the reasoning behind low relief prevalence. The first possibility is that *Antidorcas* have a phylogenetic predisposition towards low relief (e.g. Fraser et al. 2018). Alternatively, researcher subjectivity, promotes low relief. This alternative seems unlikely when considering 90% of the dentition scored belonged to *Antidorcas*, and the scores were given relative to each other (e.g. rather than relative to taxa with larger dentition). The remaining alternative is that the low relief dominance is a true reflection of dietary preference and vegetation cover, showing *Antidorcas* to be subject to a highly abrasive diet throughout this temporal range. As low-level feeders, *Antidorcas* are likely to ingest higher levels of grit than animals feeding at higher levels, the inclusion of

grit during mastication has been linked to lower occlusal relief in herbivores (Kaiser et al. 2013).

Assuming mesowear is reflective of dietary preference and, therefore, vegetation cover, local variation is evident from the differential percentages of mesowear variables in members. Sterkfontein Member 5 and Swartkrans Member 1 are considered roughly contemporary but appear to display contrasting mesowear signals from *Antidorcas*. This could be highlighting local vegetation differences or be a reflection of biotic interactions and niche separation of *Antidorcas* populations (intra- or inter-specifically) at Sterkfontein and Swartkrans differentially. However, 'Swartkrans Member 1' contains material of unknown exact provenance (mixed from the lower bank and hanging remnant). When stratigraphically separated, Swartkrans Member 1 hanging remnant and Sterkfontein Member 5 West (c. 1.7-1.5 Ma) *Antidorcas* yields 100% low relief and rounded cusp dominance. Further, the slightly older Sterkfontein Member 5 East and Swartkrans Member 1 lower bank *Antidorcas*, show low relief, rounded cusp dominance. This trend is evident from both upper and lower molars, apart from for Swartkrans Member 1 lower bank. Swartkrans Member 1 lower bank *Antidorcas* is dominated by high relief, sharp cusps from upper molars, reflective of a browse-dominated diet. The low relief and rounding of cusps suggests high abrasion, whilst the lower molars are more prone to blunting than upper molars, it only appears to be the case for Swartkrans Member 1 Lower Bank. This may suggest that Swartkrans M1 LB *Antidorcas* had a *slightly* greater browse component in the diet, with more woodland present during deposition of this Member.

Mesowear signal through time when split by species

The results here highlight the possibility of an averaged signal if using multiple species and the importance of accurate taxonomic identification prior to mesowear analysis, to prevent species/ dietary averaging skewing the palaeoenvironmental signal.

Although species differences are apparent in mesowear variables, these differences are only significant for **Swartkrans Member 2**. If the species were indeed present at the same time, this may be reflective of increased character displacement of species, forcing species to specialise. Niche separation strategies of potential competitors emerge to ensure survival where resources are less readily available. Similar has been found in modern springbok, when compared to potentially competing gemsbok (*Oryx gazella*) in semi-desert conditions (Lehmann 2015). It is likely that each *Antidorcas* species adopts a slightly differing diet within a heterogeneous habitat landscape, such as is suggested for Swartkrans Member 2. However, the different *Antidorcas* species may not be contemporaneous but rather reflect different temporal populations, perhaps indicative of seasonal occupation according to preferred vegetation presence.

Both *A. recki* and *A. bondi* show increased dietary abrasiveness for Swartkrans Member 2. Although they differ significantly from each other, both display rounded cusp shape and low occlusal relief, which is particularly unusual for the typically- browsing *A. recki*. Mesowear, as an averaged lifetime dietary signal here, may reflect the incorporation of a slightly greater grass/other abrasive component in the diet throughout the lifetime of the *A.*

recki and *A. bondi* individuals. This is reflective of the temporal range on a regional scale (rather than a local reflection of Swartkrans palaeoevegetation).

Although often predominantly browsing within their mixed-feeding diet (as A. *recki*), modern *Antidorcas* will feed on fresh grasses following the rains, prior to grass lignification (Skinner and Louw 1996). If true also for the ancestral springbok (*A. recki*), this potential increase in grazing could reflect increased moisture during the temporal period of Swartkrans Member 2 accumulation, with the opportunistic increase in grass consumption.

High occlusal relief and rounded cusps have been positively correlated with mean annual precipitation, water balance and humidity in a study by Kaiser and Schulz (2006), whilst low relief and blunt cusps were negatively correlated, implying that mesowear can be indicative of more than simply diet but also making the picture obtainable more complex to interpret.

Table 8.34: Dominant (most frequently occurring) mesowear trait for each Antidorcas species through time. Abbreviations as follows: Provenance: SK= Sterkfontein, M=Member (with corresponding number or letter), K=Kromdraai, SKX=Swartkrans, G=Gondolin, CC=Cooper's Cave, PL=Plovers Lake, CoH= Cave of Hearths, GL=Gladysvale. Mesowear categories: L=Low relief, H= High relief, S= Sharp cusps, R=Rounded cusps, B=Blunt cusps. Where mesowear variables have equal weighting, both are given here. Upper and lower refers to maxillary and mandibular dentition respectively. Green cells highlight abrasive diets, orange highlights attrition-dominated diets.

Provenance	*A. recki*		*A. bondi*		*A. marsupialis*	
	Upper	Lower	Upper	Lower	Upper	Lower
SK M4	LR	H/LS	X	LR	X	X
KW	LB	LB	X	X	HB	X
KE/D	HR	LS	X	X	X	X
SK M5	LR	LS/R	LR	LR	LB	LS
SK M5E	X	LR	X	H/L R/S	X	X
SK M5W	LB	LB/R	LS/B	LR	X	X
SKX M1	LB	LB	X	HR	LB	HR
SKX M1 LB	X	LR	X	LR	HB	H/LS
SKX M1 HR	X	X	X	LR	X	X
KA	LB	LS	LR	LR/S	X	X
GA	X	X	X	X	LR/B	X
SKX M2	LS	LR	LR	H/LR	LB	LR
CC	LB	HS	X	X	X	X
SKX M3	LS	LR	LR/B	H/LR	HR	LR
SK LC	X	X	X	LB	X	X
SK PM6	X	X	LB	X	X	X
PL	LB/S	LS	LB	LB/R/S	LR	LS
CoH	X	X	LR	HS	H/LB	LR
GL	X	LR/S	X	X	X	X

8.5 SUMMARY

Problems with using the mesowear method to accurately reflect diet and palaeoenvironmental factors were found and many apparent contradictions in dietary signal arose. The method was tested further with a few small experiments (Appendix A7) and creating additional categories to incorporate the range of variation indicative of mixed-feeding practices as far as possible and to seek the source of error. Further mesowear categories would be beneficial for future studies, including a 'medium relief' category as well as categories beyond relief and cusp shape.

In spite of the issues found, the following palaeodietary indicators were apparent:

- Consistent with previous studies (e.g. Fortelius and Solounias 2000; Kaiser and Schulz 2006; Blondel et al. 2010), upper molars presented a greater browsing signal than lower molars, lower molars tended towards blunting.

-Swartkrans Member 2 (c. 1.7 Ma) shows dietary deviation from typical *Antidorcas* palaeoecology.

-Swartkrans Member 2 shows more grazing/ abrasion dominated diets than indicated by other methods (e.g. microwear, see chapter 9), which emphasise a stronger browsing component. This may reflect the grazing diet of *A. bondi* (mesowear) which dominates the Swartkrans Member 2 assemblage, yet *A. bondi* may become reliant on fallback foods of increased browse prior to death (DMTA, see next chapter).

-*A. bondi* displays more variation in new mesowear scores through time than any other *Antidorcas* species. This is unexpected from morphological indicators that would suggest stronger selection pressure towards grazing for *A. bondi* than for the other, mixed feeding *Antidorcas* species.

- By Cave of Hearths deposition (c. 0.6 Ma), *A. bondi* displays fewer incidences of grazing, with a greater prevalence of high occlusal relief and sharp cusps. This result may be slightly skewed by the increased incidence of younger individuals (in spite of very young and very old being excluded from the analysis).

- *Antidorcas* shows a tendency towards low relief, possibly indicative of low-level feeding and the inclusion of grit during mastication, and/or a highly abrasive diet. No directional dietary transition through time is apparent for the *Antidorcas* genus as a whole or when considered as separate species (Table 8.11; Table 8.25; Table 8.33).

- *A. recki* (maxillary and mandibular dentition alike) display low relief and sharp cusps as the dominant mesowear signal, indicating a mixed-feeding to browsing diet.

- *A. bondi* (maxillary and mandibular dentition alike) display low relief and rounded cusps as the dominant mesowear signal, indicating a grazing to mixed-feeding diet.

- Fossil *A. marsupialis* (maxillary and mandibular dentition alike) display almost equal high and low relief, with a slight dominance of low relief. Sharp cusps prevail for maxillary molars, while mandibular molars tend towards rounding.

CHAPTER 9

DMTA: Microwear

9.1 INTRODUCTION

Microscopic use-wear scars left on *Antidorcas* dental enamel surfaces, by vegetation consumed during the last few days/weeks of the animals' life, are explored in this chapter. Microwear initially indicates the animals' ecological position along a grazing to browsing dietary spectrum. This is achieved via the microscopic wear patterns caused by food

particles (grass/browse) dragged across the occlusal surface of the tooth during mastication (Solounias et al. 1988; Teaford 1988; Solounias and Moelleken 1993; Grine et al. 2002; Figure 4.19). As with mesowear, exogenous particles, such as dust and grit undoubtedly play a part (e.g. Wood 2013), although the impact of such particles appear *relatively* minor (Merceron et al. 2016). The dental microwear texture analysis (DMTA) approach used here enables a deeper insight into the feeding habits of *Antidorcas*, beyond that of simply grazing versus browsing diets (see chapter 4).

In this chapter, the development of the DMTA method, and its use in palaeoenvironmental reconstruction and palaeoecological contexts will be discussed. Subsequently, this method's application to South African *Antidorcas* is analysed and evaluated. The impact of individual animal preference is considered initially to explore how the method can inform on diet; and subsequently ensure conclusions regarding *Antidorcas* palaeoecology, palaeovegetation and palaeoenvironment are as reflective of these factors as possible. *Antidorcas*, as a genus, is then used to evaluate palaeovegetation change through time (with cave deposit members ordered chronologically; relative chronology is outlined in chapters 2 (Table 2.2) as evidenced by DMTA. The *Antidorcas* dataset is then split specifically to assess *Antidorcas* species palaeoecology and any species-level dietary change through time. These trends are contrasted against the supplementary obligate-grazing and obligate-browsing species from modern contexts and from each member (where present) to establish the grazing-browsing parameters for each DMTA variable.

9.2 RESULTS

DMTA data was initially subject to non-parametric statistical analysis tests due to being not normally distributed and having only small sample sizes for each species in each member (Francisco et al. 2018). To correlate with published microwear results more closely parametric tests (one-way ANOVA with post-hoc Tukey's HSD and Fisher's LSD tests) were also performed on rank-transformed microwear variables. This is done once to establish species dietary differences and a second time to understand dietary differences (for all *Antidorcas* species combined) between members. The method and its analysis are continually being tested and refined (e.g. Francisco et al. 2018; Ramdarshan et al. 2016, 2017; Merceron et al. 2010, 2018) and it is worth using multiple statistical approaches in this instance to ensure sufficient accuracy and repeatability.

The sample of '*A. australis*' (see chapter 4 'DMTA') has considerable intra-specific variation (standard deviation) and much higher Smc values than the other species (Table 9.2). Standard deviation (SD) in Smc shows great variability for Swartkrans Member 2 (Table 9.4).

In the following Tables and Figures, provenance member deposits are separated as far as possible based on the information available, for instance, Swartkrans Member 1 material unable to be distinguished to either Member 1 lower breccia or hanging remnant, was combined as 'Member 1'. This was due to the ongoing curation of the material and lack of time to personally investigate this specific provenance data further whilst in South Africa. It is acknowledged that this is likely to average and confuse the signal for this time period, with future work advised to seek this provenance information where available.

9.2.1 Modern *Antidorcas*

In order to accurately interpret results of the fossil enamel surfaces it is useful to establish expected parameters from a known modern subset.

Tables giving the descriptive statistics for modern *A. marsupialis* DMTA and summary DMTA statistics for *A. marsupialis* according to known sex, separated to assess dietary sexual dimorphism is included in *Antidorcas* summary chapter (Chapter 6, Table 6.13 and 6.14).

Table 9.1 summarises the mean values for each DMTA variable for taxa belonging to the major feeding categories. Modern *Antidorcas marsupialis* mean values are indicative of browse-dominated mixed-feeding dietary parameters. Minimal dietary sexual dimorphism is apparent from DMTA variables. High Tfv values and a wide range of Tfv values are shown by modern *A. marsupialis,* indicative of mixed-feeding diets.

The browsing component of modern *A. marsupialis*' diet may be vulnerable to being overemphasised via DMTA variables. This is because although springbok do browse, they do so primarily following the rains, feeding on new shoots prior to lignification (Skinner and Louw 1996). Newer grasses have been shown to leave only trace microwear signals, compared to mature grasses (Massey et al. 2008; Francisco et al. 2018).

When extrapolating back to fossil *Antidorcas*, C_3 grasses (indicative of closed habitats) are believed to leave finer scratches on the dental enamel surface than C_4 grasses (indicative of more open habitats). This is due to the high phytolith content and comparative coarseness of C_4 grasses compared to C_3 grasses. As introduced earlier (see chapter 4), the possibility exists that the finer C_3-induced scratches will be overwritten more easily and regularly (Solounias and Semprebon 2002) for fossil *Antidorcas* than would be true for obligate grazers (who would typically favour C_4 grasses), masking the grazing element of *Antidorcas'* palaeodiet.

However, as *Antidorcas* palaeoecology is not the primary research objective here, but rather used as an indication of palaeovegetation and palaeoenvironmental conditions, the difference between C_3 (closed habitats, wetter conditions) and C_4 (open habitats, more arid conditions) dominance should still be apparent via fossil *Antidorcas* diet. The difference would be visible through a divergence of browsing (indicative of more closed C_3 habitats) and grazing (indicative of more open C_4 habitats), irrespective of whether *Antidorcas* consumes grasses growing in closed habitats.

Table 9.1: Microwear values for modern species of known diet. Data for Alcelaphus buselaphus, Cephalophus sylvicultor, Giraffa Camelopardalis and Syncerus caffer supplied by Dr Gildas Merceron from the data set owned by the Laboratoire du Paléontologie, Évolution, Paléoécosystems, Paléoprimatologie (PALEVOPRIM), Université de Poitiers (2018).

Species	Diet	N	Mean Asfc(1om)	Mean epLsar ($1.80\mu m \times 10^{-3}$)	Mean HAsfc 9cell	Mean HAsfc 81cell	Mean Tfv (μm^3)	Mean Smc
Alcelaphus buselaphus	Grazer	27	1.58	6.04	0.33	0.58	41469.52	0.52
Syncerus caffer	Grazer	35	1.56	5.26	0.32	0.58	35647.17	0.39
Cephalophus sylvicultor	Fruit browser	28	3.84	3.11	0.34	0.61	34675.67	0.49
Giraffa camelopardalis	Leaf browser	15	2.03	1.81	0.40	0.68	24860.20	0.49

9.2.2 Fossil *Antidorcas*

Table 9.2: Summary dental microwear texture parameter statistics. Mean (M), standard deviation (SD) and standard error of the mean (SEM) for each Antidorcas species. Antidorcas sp. refers to those identifiable only to genus level. F=Fossil, M=Male.

Species	N	Asfc			epLsar ($x10^{-3}$)			HAsfc 9			HAsfc 81			Tfv2			Smc		
		M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM
Fossil																			
Antidorcas sp.	24	7.25	6.73	1.37	2.24	1.68	3.42	0.53	0.33	0.07	0.83	0.44	0.09	40494.50	10197.97	2081.65	0.14	0.19	0.04
A. recki	26	5.81	3.85	0.75	2.68	1.80	3.53	0.49	0.47	0.09	0.86	0.57	0.11	43549.07	7086.40	1389.76	0.17	0.12	0.02
A. bondi	44	5.51	4.07	0.61	2.86	1.77	2.67	0.47	0.32	0.05	0.83	0.44	0.07	40880.83	9408.36	1418.36	0.21	0.45	0.07
A. marsupialis	30	5.15	4.35	0.79	2.89	1.64	0.30	0.44	0.26	0.05	0.73	0.34	0.06	38808.41	9916.63	1810.52	0.13	0.07	0.01
'A. australis'	10	5.48	5.84	1.85	3.40	2.00	6.34	0.56	0.32	0.10	1.04	0.64	0.20	48927.53	8373.22	2647.85	10.05	23.75	7.51
Modern																			
A. marsupialis	43	4.10	3.94	0.60	3.43	1.70	2.59	0.54	0.33	0.05	1.02	0.62	0.09	42010.27	11510.90	1755.40	0.19	0.23	0.04

*Table 9.3: DMTA descriptive statistics (N=number of individuals; M=mean; SD=standard deviation; SEM=standard error of the mean) for the Antidorcas genus for each time period, as represented by the provenance cave deposit Member. SK=Sterkfontein (*unstrat=unstratified); K=Kromdraai; SKX=Swarkrans; GD=Gondolin; CC=Cooper's Cave; CoH=Cave of Hearths. Variables measured in µm.*

Provenance	N	Asfc			epLsar (x10^{-3})			HAsfc 9			HAsfc 81			Tfv2			Smc		
		M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM
Sk M 4	8	9.22	2.28	0.8	1.57	1.06	0.38	0.43	0.25	0.09	0.89	0.44	0.16	43417.93	6282.11	2221.06	0.16	0.11	0.04
Sk M5	6	2.15	0.82	0.34	2.83	1.74	0.71	0.23	0.08	0.03	0.55	0.2	0.08	44286.88	7285.16	2974.15	0.47	0.37	0.15
Sk unstrat.	2	2.09	0.49	0.35	4.48	1.71	0.90	1.11	0.85	0.60	1.71	1.22	0.86	43041.72	3335.89	2358.83	0.13	0.00	0.00
KA	11	5.49	5.05	1.52	3.67	2.49	0.75	0.42	0.26	0.08	0.77	0.41	0.12	44897.53	10831.12	3265.71	2.49	7.83	2.36
KW	7	2.32	1.01	0.38	4.12	1.85	0.70	0.36	0.13	0.05	0.6	0.13	0.05	42725.21	4445.80	1680.35	0.18	0.08	0.03
KE	2	3.42	2.31	1.64	3.02	0.84	0.59	0.55	0.02	0.01	1.35	0.82	0.58	43157.25	4950.41	3500.47	0.14	0.09	0.07
SKX M1	9	2.52	1.07	0.36	3.48	1.28	0.43	0.61	0.29	0.10	0.92	0.56	0.19	39596.73	8653.96	2884.65	0.08	0.02	0.01
SKX M2	48	7.17	5.82	0.84	2.08	1.37	0.20	0.45	0.21	0.03	0.74	0.26	0.04	4.956.74	10199.82	1472.22	1.65	10.59	1.53
SKX M3	12	3.79	3.44	0.99	2.96	1.76	0.51	0.41	0.14	0.04	0.7	0.23	0.07	40147.62	8847.75	2554.13	0.36	0.84	0.24
GDA	1	3.7	x	x	1.87	x	x	0.15	x	x	0.52	x	x	45289.08	x	x	0.74	x	x
CC	3	3.76	1.19	0.69	3.76	2.87	1.20	0.98	1.36	0.79	1.21	1.48	0.85	47510.96	14611.90	8436.18	0.09	0.03	0.02
CoH	24	6.96	4.23	0.86	2.98	1.83	0.37	0.61	0.42	0.09	1.03	0.57	0.12	38984.13	10553.30	2154.18	0.14	0.11	0.02

Table 9.4: Descriptive statistics (M=mean, SD=standard deviation, SEM=standard error of the mean) for dental microwear variables for each species (Antidorcas and supplementary) in each deposit. Modern data for Alcelaphus buselaphus, Cephalophus sylvicultor, Giraffa Camelopardalis and Syncerus caffer supplied by Dr Gildas Merceron from the data set owned by the Laboratoire du Paléontologie, Évolution, Paléoécosystems, Paléoprimatologie (PALEVOPRIM), Université de Poitiers (2018). Variables measured in µm.

Provenance and Species	N	Asfc			epLsar (x10-3)			HAsfc 9			HAsfc 81			Tfv2			Smc		
		M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM	M	SD	SEM
Sterkfontein Member 4																			

Provenance and Species	N	Asfc			epLsar (x10-3)			HAsfc 9			HAsfc 81			Tfv2			Smc		
		M	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**
A. recki	8	**9.22**	2.28	0.80	**1.57**	1.06	0.38	**0.43**	0.25	0.09	**0.89**	0.44	0.16	**43417.93**	6282.11	2221.06	**0.16**	0.11	0.04
T.strepsiceros	1	**2.03**	x	x	**3.33**	x	x	**0.39**	x	x	**0.60**	x	x	**37559.13**	x	x	**0.13**	x	x
D.pygargus	1	**1.90**	x	x	**3.21**	x	x	**0.27**	x	x	**0.60**	x	x	**34761.55**	x	x	**0.21**	x	x
M.broomi	2	**1.44**	0.58	0.41	**2.08**	1.59	1.12	**0.43**	0.17	0.12	**0.69**	0.25	0.17	**45141.56**	2247.15	1588.97	**0.60**	0.10	0.07
Sterkfontein Member 5																			
A.bondi	5	**2.34**	0.75	0.33	**2.35**	1.42	0.64	**0.25**	0.07	0.03	**0.59**	0.18	0.08	**45912.44**	6820.81	3050.36	**0.36**	0.28	0.13
D.pygargus	2	**4.89**	3.43	2.43	**3.73**	3.55	2.51	**0.54**	0.19	0.14	**0.68**	0.16	0.12	**47498.62**	6947.57	4912.68	**0.14**	0.09	0.07
Sterkfontein unstratified																			
D.pygargus	6	**3.52**	1.22	0.50	**2.63**	0.90	0.37	**0.53**	0.18	0.07	**0.79**	0.21	0.09	**37618.84**	6969.76	2845.39	**0.14**	0.07	0.06
Kromdraai A																			
A.recki	3	**7.21**	7.64	4.41	**1.08**	0.06	0.37	**0.28**	0.04	0.02	**0.56**	0.17	0.17	**44950.55**	8058.52	4652.59	**0.22**	0.13	0.07
A.bondi	5	**5.63**	5.28	2.36	**5.11**	2.23	1.00	**0.39**	0.22	0.10	**0.63**	0.20	0.09	**42470.00**	12442.96	5564.66	**0.09**	0.03	0.01
'A.australis'	3	**3.53**	1.77	1.02	**3.85**	2.32	1.34	**0.62**	0.38	0.22	**1.22**	0.54	0.31	**48890.40**	13165.15	7600.9	**8.75**	15.02	8.67
Kromdraai W																			
A.recki	6	**2.35**	1.10	0.45	**4.60**	1.47	0.60	**0.35**	0.14	0.06	**0.62**	0.14	0.06	**43660.15**	4046.67	1652.04	**0.19**	0.09	0.04

Provenance and Species	N	Asfc			epLsar (x10-3)			HAsfc 9			HAsfc 81			Tfv2			Smc		
		M	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**
A.marsupialis	1	**2.14**	x	x	**1.22**	x	x	**0.46**	x	x	**0.48**	x	x	**37115.54**	x	x	**0.13**	x	x
D.pygargus	3	**2.89**	0.61	0.35	**4.25**	0.72	0.42	**0.34**	0.08	0.04	**0.53**	0.19	0.11	**37028.65**	16880.89	9746.19	**0.35**	0.30	0.17
T.strepsiceros	1	**0.75**	x	x	**2.56**	x	x	**0.11**	x	x	**0.27**	x	x	**1598.83**	x	x	**0.53**	x	x
Kromdraai E																			
A.recki	1	**5.06**	x	x	**3.61**	x	x	**0.57**	x	x	**1.94**	x	x	**39656.78**	x	x	**0.07**	x	x
A.marsupialis	1	**1.79**	x	x	**2.43**	x	x	**0.54**	x	x	**0.77**	x	x	**46657.71**	x	x	**0.21**	x	x
D.pygargus	1	**2.33**	x	x	**2.15**	x	x	**0.63**	x	x	**0.60**	x	x	**41787.70**	x	x	**0.07**	x	x
Swartkrans Member 1																			
A.recki	2	**2.71**	0.68	0.48	**3.24**	1.11	0.79	**0.81**	0.15	0.11	**0.78**	0.13	0.09	**32937.65**	2796.05	1977.11	**0.07**	0.00	0.00
A.marsupialis	3	**2.11**	1.09	0.63	**3.22**	2.16	1.25	**0.66**	0.38	0.22	**0.93**	0.50	0.29	**39288.06**	9993.49	5769.74	**0.09**	0.03	0.02
'A.australis'	3	**2.85**	1.64	0.95	**3.78**	0.95	0.55	**0.54**	0.29	0.17	**1.13**	0.92	0.53	**46494.02**	7691.11	4440.47	**0.07**	0.00	0.00
D.pygargus	2	**2.75**	0.99	0.70	**3.51**	0.38	0.27	**0.75**	0.15	0.11	**1.99**	0.70	0.49	**50324.24**	15067.02	11035.83	**0.17**	0.05	0.04
Swartkrans Member 2																			
A.bondi	23	**5.91**	4.27	0.89	**2.26**	1.17	0.24	**0.39**	0.16	0.03	**0.72**	0.20	0.04	**40835.74**	10252.32	2137.76	**0.13**	0.08	0.02
A.marsupialis	3	**3.98**	2.02	1.16	**2.53**	0.93	0.54	**0.27**	0.06	0.04	**0.52**	0.10	0.06	**36061.45**	3539.12	2043.31	**0.17**	0.12	0.07

Provenance and Species	N	Asfc			epLsar (x10-3)			HAsfc 9			HAsfc 81			Tfv2			Smc		
		M	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**
'A.australis'	3	**11.63**	8.00	4.62	**2.50**	3.16	1.83	**0.63**	0.41	0.23	**0.96**	0.70	0.40	**49472.02**	7549.82	4358.89	**24.56**	42.40	24.48
Swartkrans Member 3																			
A.recki	2	**7.28**	0.07	0.05	**1.20**	1.56	1.10	**0.40**	0	0	**0.76**	0.19	0.13	**45978.77**	2557.37	1808.33	**0.07**	0.00	0.00
A.bondi	1	**1.44**	x	x	**3.39**	x	x	**0.27**	x	x	**0.44**	x	x	**33149.02**	x	x	**3.00**	x	x
A.marsupialis	7	**3.52**	3.90	1.47	**3.46**	1.91	0.72	**0.47**	0.15	0.06	**0.72**	0.26	0.10	**38077.62**	8881.2	3356.78	**0.09**	0.03	0.01
'A.australis'	1	**0.82**	x	x	**3.59**	x	x	**0.21**	x	x	**0.48**	x	x	**54705.95**	x	x	**0.41**	x	x
D.pygargus	3	**1.46**	0.04	0.02	**2.34**	0.60	0.35	**0.23**	0.03	0.02	**0.52**	0.06	0.03	**35044.75**	8309.96	4797.76	**0.31**	0.31	0.18
Cave of Hearths																			
A.bondi	9	**7.06**	3.36	1.12	**3.28**	2.19	0.73	**0.88**	0.47	0.16	**1.40**	0.65	0.22	**38198.97**	7285.32	2428.44	**0.09**	0.03	0.01
A.marsupialis	13	**7.33**	4.99	1.39	**2.68**	1.68	0.47	**0.45**	0.31	0.09	**0.79**	0.41	0.11	**37852.97**	12488.26	3463.62	**0.14**	0.08	0.02
Gondolin GDA																			
A. marsupialis	1	**3.70**	x	x	**1.87**	x	x	**0.15**	x	x	**0.52**	x	x	**45289.08**	x	x	**0.75**	x	x
D. pygargus	2	**2.15**	0.40	0.28	**6.81**	1.20	0.85	**0.32**	0.11	0.08	**0.55**	0.06	0.04	**30466.43**	4800.97	3394.8	**0.35**	0.08	0.05
Cooper's Cave																			
A.recki	3	**3.76**	1.19	0.69	**3.76**	2.09	1.20	**0.98**	1.36	0.79	**1.21**	1.48	0.85	**47510.96**	14611.9	**8436.18**	0.09	0.03	0.02

Provenance and Species	N	Asfc			epLsar (x10-3)			HAsfc 9			HAsfc 81			Tfv2			Smc		
		M	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**	**M**	**SD**	**SEM**
Modern																			
Alcelaphus buselaphus	27	**1.58**	0.74	0.14	**6.04**	1.79	0.34	**0.33**	0.21	0.04	**0.58**	0.23	0.04	**41469.52**	11525.5	**2218.08**	0.52	0.40	0.08
Cephalophus sylvicultor	28	**3.84**	3.11	0.59	**3.11**	1.76	0.33	**0.34**	0.13	0.02	**0.61**	0.20	0.04	**34675.67**	10382.24	**1962.06**	0.49	0.58	0.11
Giraffa camelopardalis	15	**2.03**	0.91	0.24	**1.81**	1.25	0.32	**0.40**	0.09	0.34	**0.68**	0.51	0.13	**24860.2**	17714.52	**4573.87**	0.49	0.55	0.14
Syncerus caffer	35	**1.56**	0.86	0.15	**5.26**	2.37	0.40	**0.32**	0.19	0.03	**0.58**	0.29	0.05	**35647.17**	12739.77	**2153.41**	0.39	0.20	0.03
Damaliscus pygargus	14	**2.99**	1.80	0.48	**3.80**	2.00	0.53	**0.53**	0.37	0.10	**1.03**	0.58	0.15	**40671.13**	9849.84	**2632.48**	0.16	0.11	0.03
Antidorcas marsupialis	42	**3.99**	3.91	0.60	**3.40**	1.70	0.26	**0.55**	0.33	0.05	**1.03**	0.62	0.10	**41807.91**	11572.75	**1785.71**	0.19	0.23	0.04

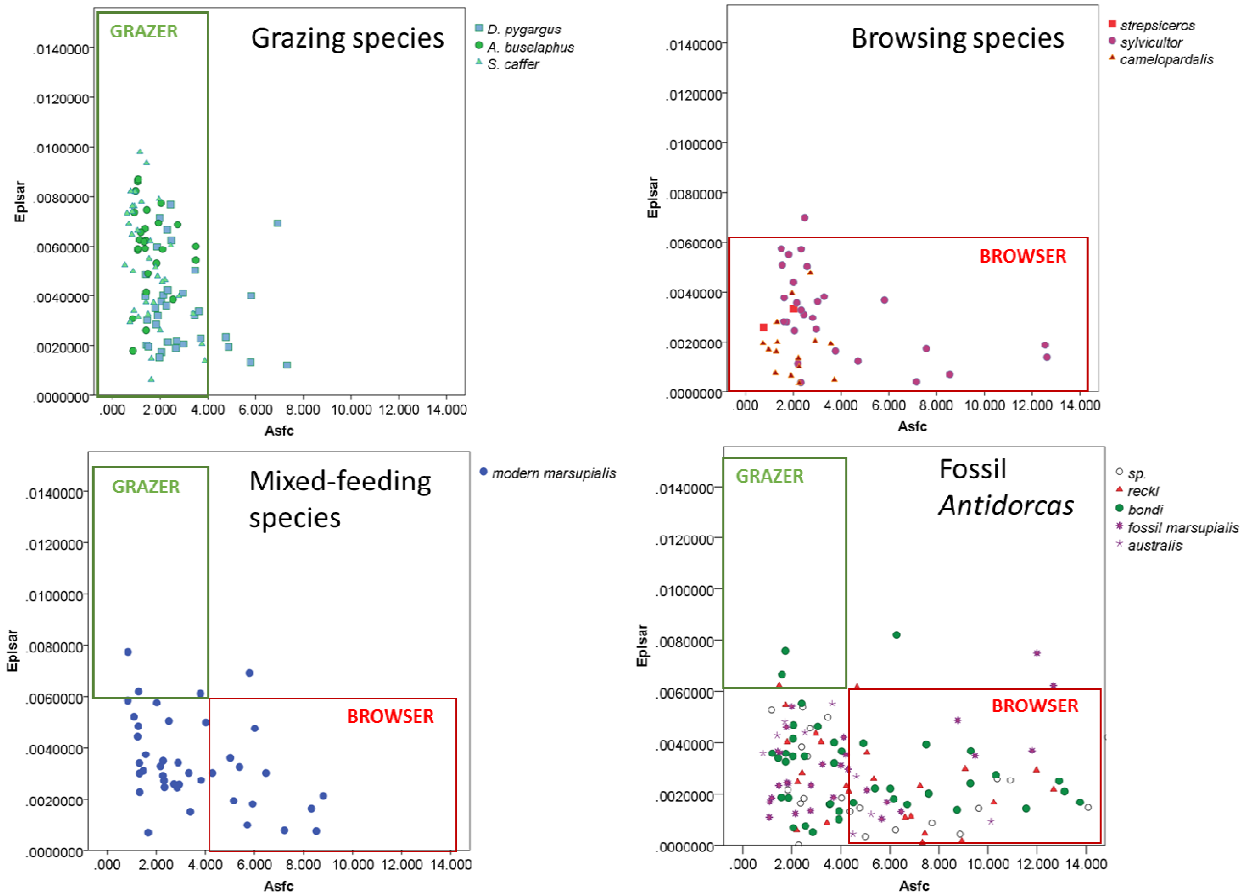


Figure 9.1: Biplots (Asfc on X axis vs epLsar on Y axis) of modern ruminants (obligate grazers and obligate browsers) and extinct species of Antidorcas from South African Cradle of Humankind sites (Figure adapted from Sewell et al. 2019).

As found via traditional microwear methods by Solounias and Semprebon (2002), browse-dominated mixed feeders plot within the browsing eco-space and graze-dominated mixed-feeders within the grazing eco-space (Figure 9.1). Mixed-feeding may be identified via a biplot such as Figure 9.1, considering these two textural parameters (Asfc and EpLsar) but need to be explored further to understand the nature of the 'mixed-feeding' dietary practices.

The sampled modern 'mixed-feeding' species of *A. marsupialis* is actually shown to be more reliant on browse (Figure 9.1). As this biplot is an oversimplification, individuals that fall into this eco-space between grazers and browsers but within modern ranges of either/both, require consideration of all DMTA parameters (beyond Asfc versus epLsar) to accurately assess their palaeoecology.

9.2.2.1 Individual Animal Variation

DMTA signals from a few selected individuals are evaluated here to assess the degree of individual animal variation within the sample. Figure 9.1 highlights how individual variation can skew the overall species dietary signal. A mixed-feeding species may be a collection of grazers and browsers, or a group of mixed-feeding individuals, alternating between graze (old/new grass shoots of varying heights) and browse (fruit and/or leaf browsers) on a daily or seasonal basis.

Sterkfontein Member 5 [c. 1.7-0.8 Ma]

Two individuals with 'clear microwear signals' ('clear' from the photosimulations produced via the LeicaMap microwear analysis software) are evaluated here to understand the detail available from DMTA.

SF992: *Antidorcas bondi* 'grazer'

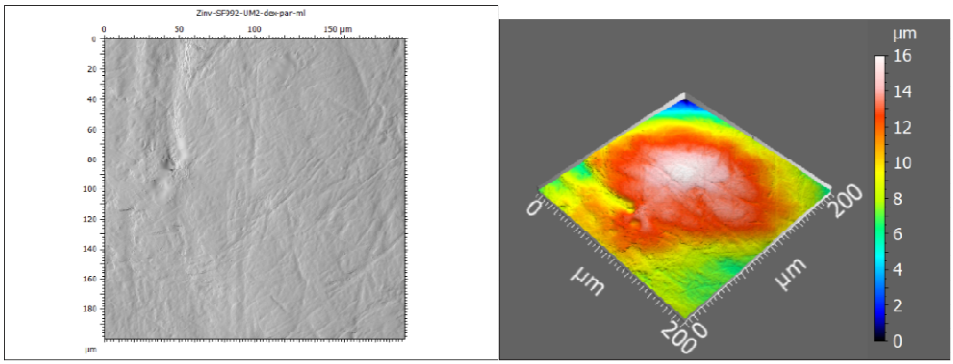


Figure 9.2: Typical grazing signal photosimulation and textural scale for SF 992, right M^2 paracone. Sterkfontein Member 5 Antidorcas bondi.

The paracone of SF 992 (Figure 9.2) shows low complexity (2.31µm Asfc), within the range of grazing bovids but also low anisotropy (2.90 x 10^{-3} µm epLsar), and relatively high heterogeneity (9 cell= 0.41µm; 81 cell=0.59µm HAsfc) (at a relatively fine scale, Smc=0.30µm), showing SF 992 to be within the range of a mixed feeder.

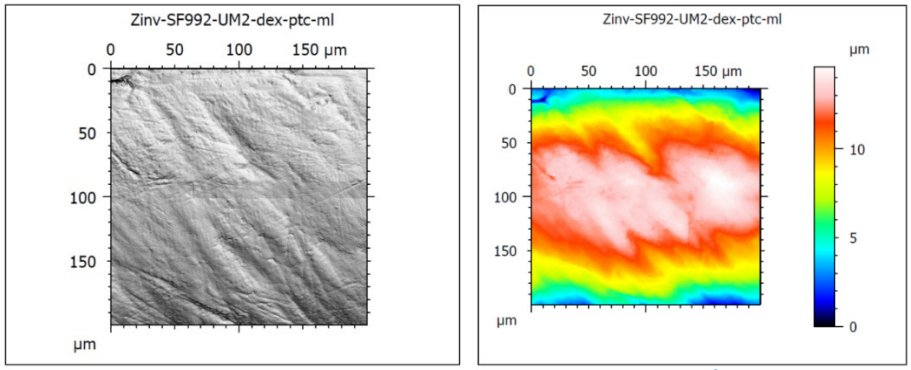


Figure 9.3: Photosimulation and textural scale for SF 992 right M^2 protocone. Sterkfontein Member 5 Antidorcas bondi.

The protocone of SF 992 however, shows a clear grazing signal, with low complexity (1.67µm Asfc) and high anisotropy (7.80 $x10^{-3}$µm epLsar) but with relatively high heterogeneity (9 cell= 0.49µm; 81 cell=0.83µm HAsfc) (at a mid-range scale, Smc=0.41µm). Consideration of the facets used has been addressed by Ramdarshan et al. (2016, 2017), which underpinned the choice of facets used in this study. Only protocones (upper molars) and protoconids (lower molars) were combined for analysis, paracones from the same individuals were scanned but their values were not taken forward for analysis at this point (due to the combined protocone/protoconid samples yielding a larger dataset). The paracone is perhaps reflective of a slightly longer timeframe (days-weeks) than the protocone (hours-days) (Danowitz et al. 2016). For the paracone, throughout subsequent mastication on food particles, the browsing signals (e.g. deep pits) tend to preserve longer than the grazing (e.g. fine scratches) because they leave a greater scar on the enamel surface. That the paracone shows a mixed feeding signal and the protocone a grazing signal perhaps indicates the inclusion of browse in the diet less recently than grass consumption. This highlights the merits of using DMTA rather than simple microwear (2D) analysis, which would categorise this individual as a grazer, based on the scratches in this image, without fully examining the intricacies that dental microwear variables can inform on for intra-specific and individual animal palaeoecology.

As discussed in the introduction to DMTA (chapter 4), the concept of overwriting links to the abrasiveness of the diet. More abrasive diets are more regularly overwritten (Schulz et al. 2013), further making grazing signal more susceptible to overwriting.

SF 890: *Antidorcas bondi* 'mixed-feeder'

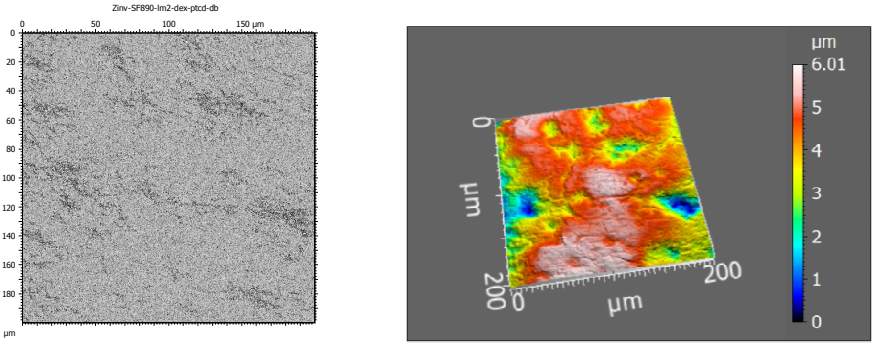


Figure 9.4: Typical browsing signal photosimulation and textural scale for SF 890 right M_2. Sterkfontein Member 5, Antidorcas bondi.

SF 890 shows low complexity (1.564µm) and low anisotropy (1.87x10^{-3}µm), placing it within the bottom left corner of a biplot of Asfc against epLsar (Figure 9.4) Taken together

with the heterogeneity values (9 cell= 0.19µm, 81 cell=0.47µm) at a relatively coarse scale (Smc 0.83µm), this is a typical mixed-feeding DMTA signal.

Swartkrans Member 1 [c. 2.0-1.4 Ma]

SKX 12067: *Antidorcas bondi* 'Variable grazer'

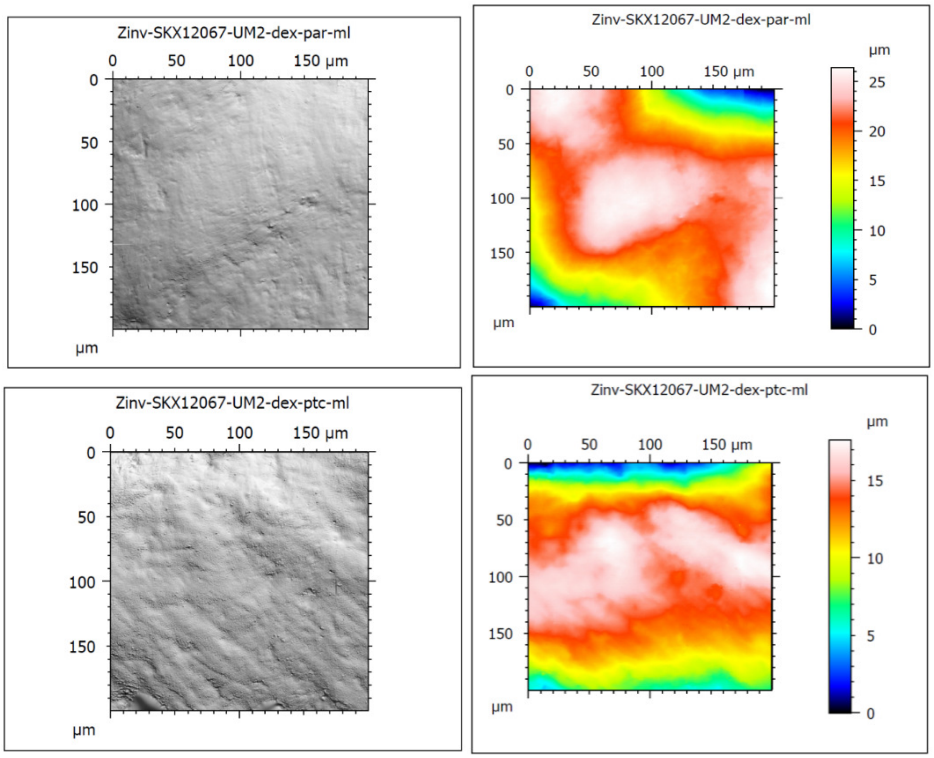


Figure 9.5: Photosimulation and textural scale for SKX 12067 paracone (top image) and protocone (lower image).

SKX12067 protocone has low complexity (2.52µm) but also low anisotropy (4.38x10^{-3}µm). Heterogeneity values are moderately low (9 cell= 0.28µm, 81 cell=0.45µm) at a fine scale (Smc 0.07µm), SKX12067 has mixed-feeding DMTA values, tending towards grazing.

Swartkrans Member 2 [c. 1.7-1.07 Ma]

SK 10555: *Antidorcas* sp. 'mixed feeder'.

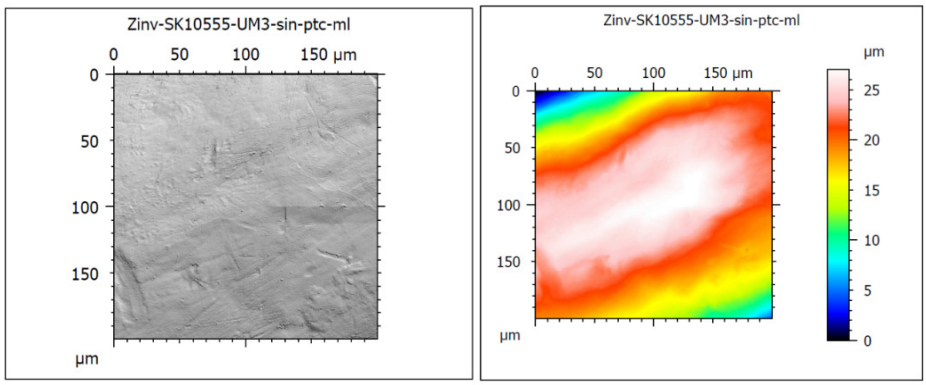


Figure 9.6: Photosimulation and textural scale for SK 105555 protocone.

SK 10555 shows low complexity (2.36µm) but also low anisotropy (1.62x10^{-3}µm). Heterogeneity values are relatively high (9 cell= 0.49µm, 81 cell=0.74µm) at a fine scale (Smc 0.07µm), SK 11073 displays mixed-feeding DMTA values.

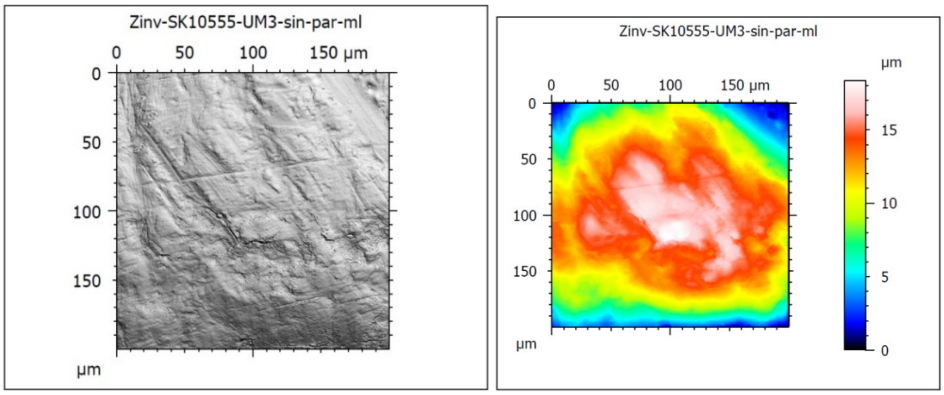


Figure 9.7: Photosimulation and textural scale for SK 10555 paracone.

SK 11073: *Antidorcas recki* 'browser'

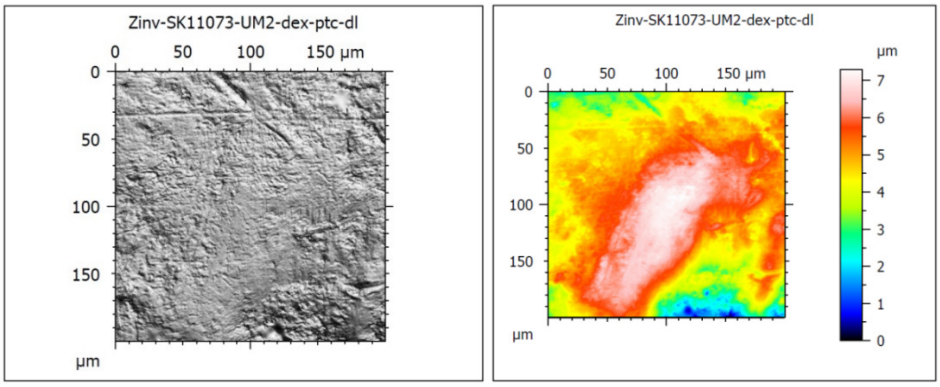


Figure 9.8: Photosimulation and surface image of SK 11073 protocone.

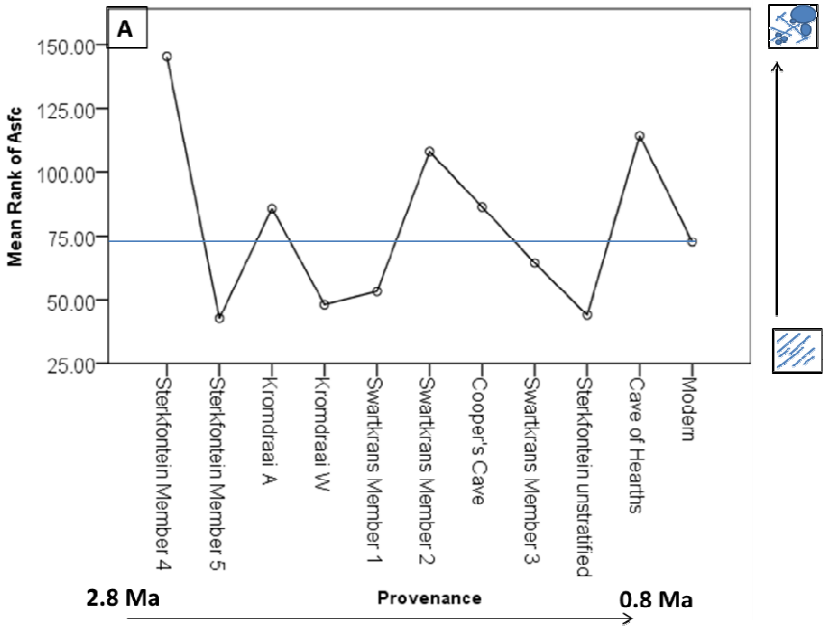
SK 11073 shows fairly high complexity (4.21µm) and low anisotropy ($3.52x10^{-3}$µm). Taken with moderate heterogeneity values (9 cell= 0.34µm, 81 cell=0.56µm) at a relatively fine scale (Smc 0.13µm), SK 11073 yields a browsing DMTA signal.

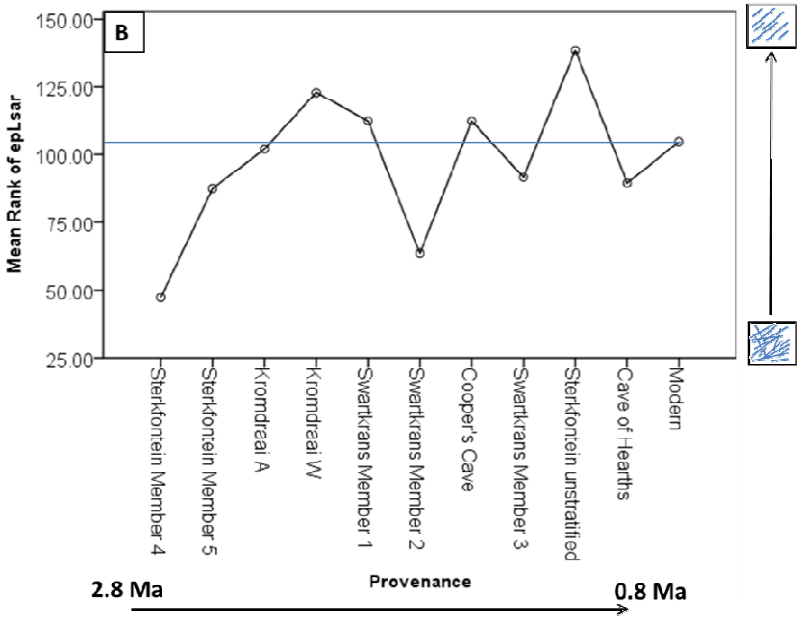
9.2.2.2 Change Through Time

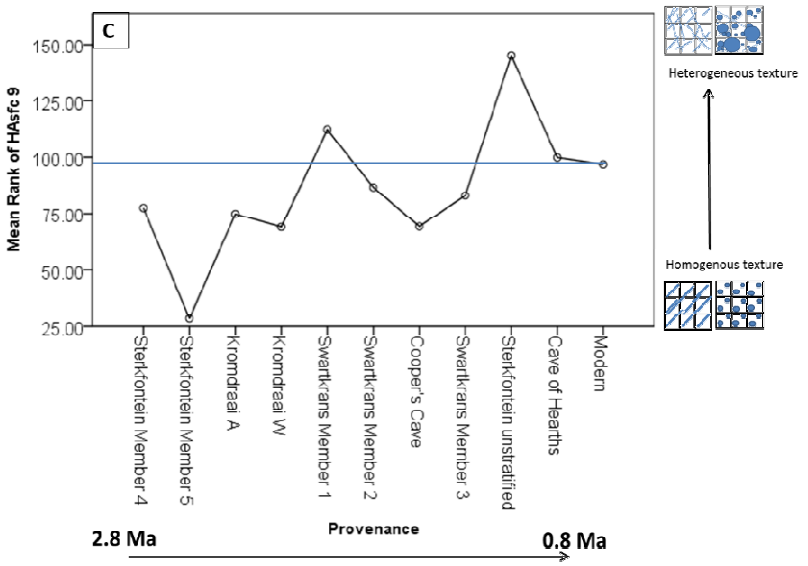
Having established the level of detail achievable for individual animals from DMTA, specimens are grouped together to establish trends through time where possible, to inform on *Antidorcas* species palaeoecology and palaeoenvironmental patterns for the South African Plio-Pleistocene.

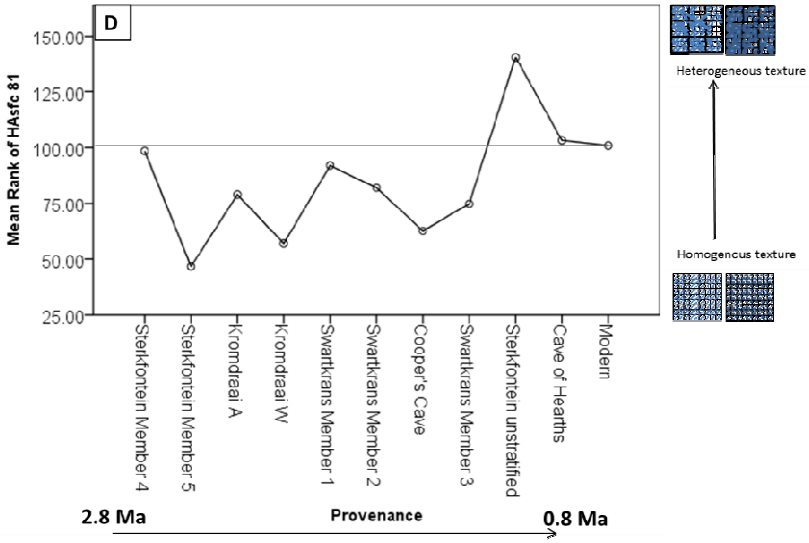
Interestingly, no significant differences were found between *Antidorcas* species (comparing each species, averaged, for the entire time period) for any microwear variable. This enabled them to be grouped as a genus to evaluate change through time. All *Antidorcas* species microwear variables were evaluated through time with non-parametric statistical analysis, using a kruskal-Wallis test (significance set to <0.05) with post-hoc Mann-Whitney U and Bonferroni adjustment (significance set at <0.001). Significant differences between provenance were found for Asfc (p<0.000), epLsar (p=0.003), HAsfc (9cell) (p=0.038) and Smc (p=0.012). No significant differences through time were found for any microwear variables for the extreme grazers (*Damaliscus pygargus*) or browsers (*Tragelaphus strepsiceros*). Although the data is not normally distributed for all microwear variables, data was rank transformed and parametric tests were calculated for comparison (see chapter

4 ‘DMTA’). The same significant differences were found using parametric ANOVA and post-hoc LSD and HSD tests.






C
Mean Rank of HAsfc 9
150.00
125.00
100.00
75.00
50.00
25.00
Sterkfontein Member 4
Sterkfontein Member 5
Kromdraai A
Kromdraai W
Swartkrans Member 1
Swartkrans Member 2
Cooper's Cave
Swartkrans Member 3
Sterkfontein unstratified
Cave of Hearths
Modern
Provenance
2.8 Ma
0.8 Ma
Heterogeneous texture
Homogenous texture


D
Mean Rank of HAsfc 81
150.00
125.00
100.00
75.00
50.00
25.00
Sterkfontein Member 4
Sterkfontein Member 5
Kromdraai A
Kromdraai W
Swartkrans Member 1
Swartkrans Member 2
Cooper's Cave
Swartkrans Member 3
Sterkfontein unstratified
Cave of Hearths
Modern
Provenance
2.8 Ma
0.8 Ma
Heterogeneous texture
Homogenous texture

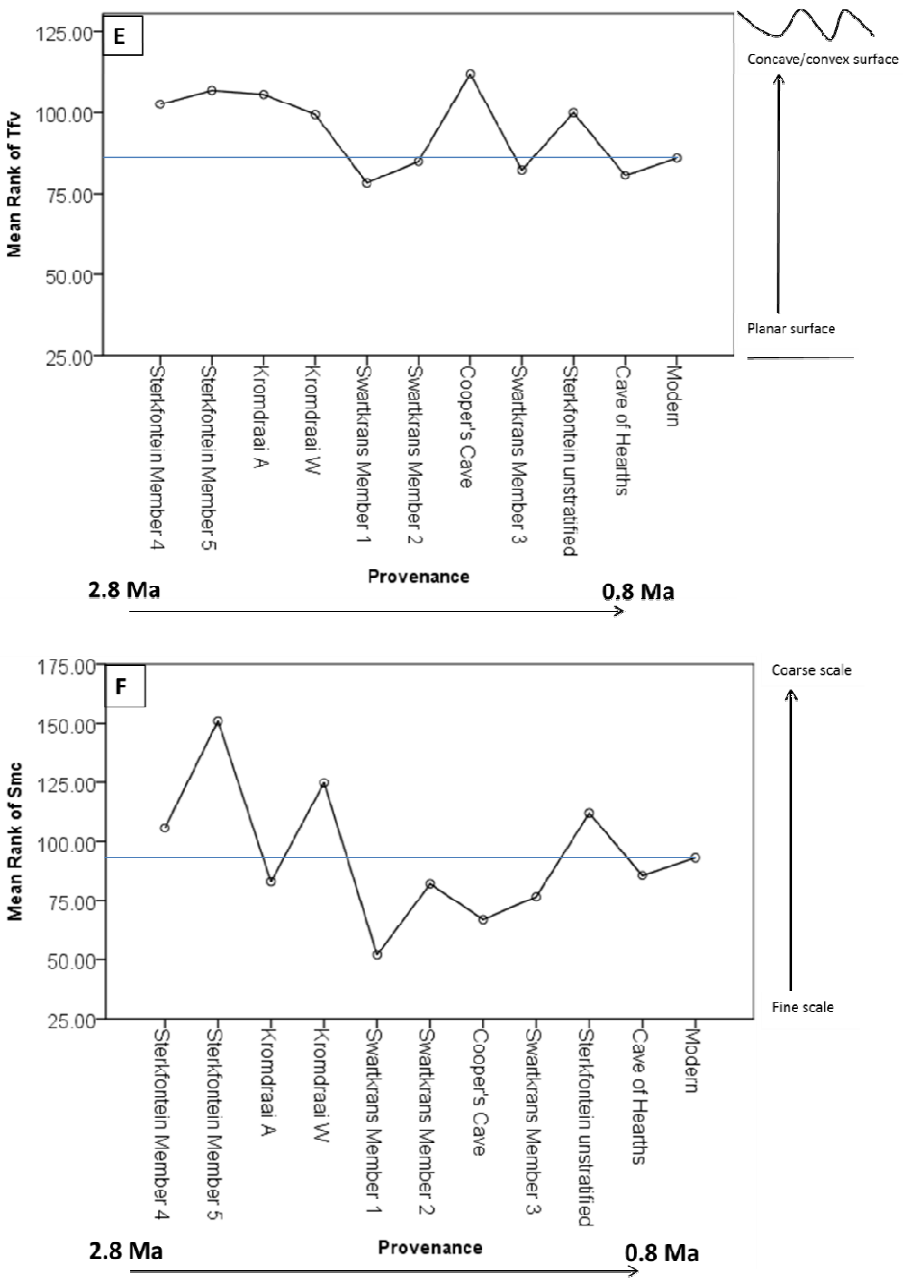


Figure 9.9: Dental microwear texture variables (A-F) through time (based on relative dates, given in chapter 3) for Antidorcas (combined as a genus). The horizontal line demarcates the relevant modern A. marsupialis value to visualise the past variation compared to modern values.

Direction of change

Post-hoc Mann-Whitney U tests revealed significance for Asfc between Sterkfontein Member 4 (N=8; rank mean=9.22 µm and Swartkrans Member 1 (N=9; rank mean=2.52µm) (p=0.001), Sterkfontein Member 4 and Kromdraai W (N=7; mean=2.31µm) (p=0.001) and Modern (N=43; mean=4.10µm) (p<0.000). Significant differences were also found for Asfc between Swartkrans Member 1 (N=9; mean=2.52µm) and Cave of Hearths (N=24; mean=6.96µm) (p=0.001); between Cave of Hearths and moderns (p=0.000) and between Swartkrans Member 2 (N=48; mean=7.17µm) and Modern (p=0.001). The only significant difference for epLsar was found between Swartkrans Member 2 (n=48, mean=2.08µm) and Moderns (n=43, mean=3.43µm) (p<0.000).

Although *Antidorcas* species combined through time showed no inter-specific differences, when considering each *Antidorcas* species separately through time (by provenance), *A. recki* (Asfc (p=0.013) and epLsar (p=0.036)) and *A.bondi* (Asfc (p=0.043), HAsfc (9cell) (p=0.018) and (81cell) (p=0.031) and Smc (p=0.004)) showed significant differences. No significant differences were found for *A. marsupialis* microwear variables through time.

Antidorcas species differences

A. recki had significantly different Asfc values from Sterkfontein Member 4 (N=8, mean=9.22 µm) to Kromdraai W (N=6, mean=2.35µm) (p=.003). Significant differences are further detailed in Table 9.5. *A. bondi* showed significant differences through time for Asfc (p=.043), HAsfc (9 cell (p=.018) and 81 cell (p=.03)) and Smc (p=.004).

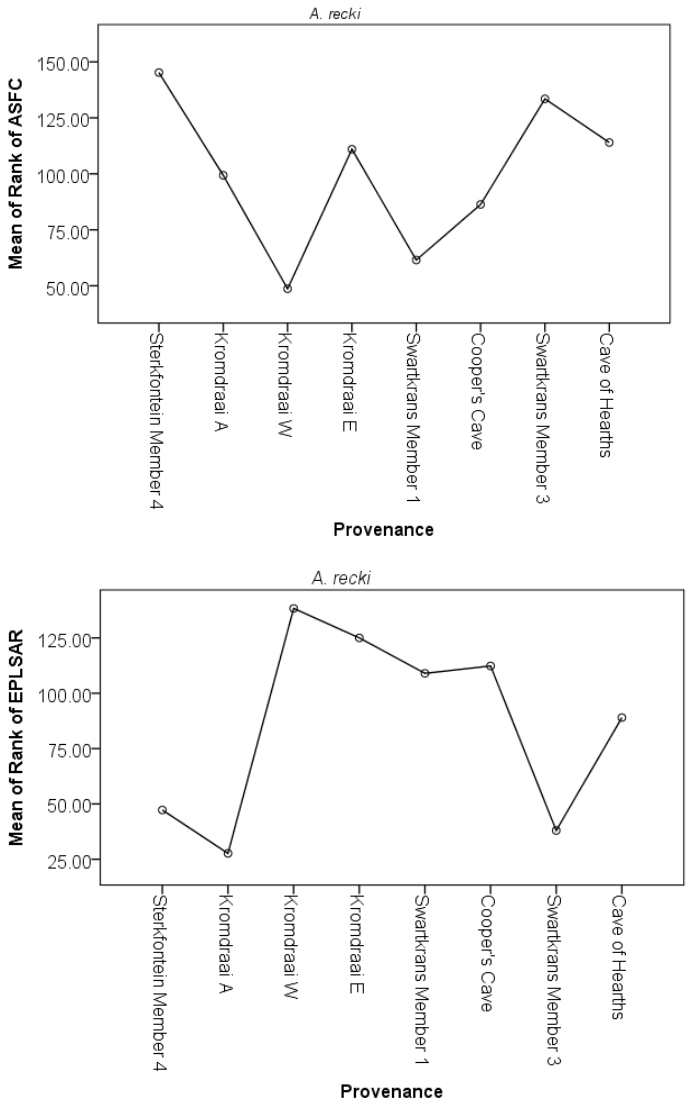


Figure 9.10: Mean complexity (Asfc) (upper image) and mean anisotropy (epLsar) (lower image) through time (by provenance with oldest deposits on the left, to the youngest on the right) for A. recki.

Table 9.5: DMTA variable pairwise comparisons significant differences for A. bondi (green text) and A. recki (red text) according to provenance member. The more conservative (HSD) appear in bold text above the diagonal and the least conservative (LSD) in regular text below the diagonal.

	SK M4	**SK M5**	**KA**	**KW**	**SKX M1**	**SKX M2**	**SKX M3**	**SK un.**	**CoH**
SK M4				***Asfc* (p=.003)**					
SK M5			**Smc (p=.004)**						
KA									**Smc (p=.011)**
KW	*epLsar* (p=.004)		*epLsar* (p=.006)						
SKX M1									
SKX M2		*Asfc* (p=.041); Smc (p=.010)							
SKX M3				*epLsar* (p=.002)					
SK un.									**HA*sfc*9 (p=.016)**
CoH		*Asfc* (p=0.009); HA*sfc* 81 (p=.006);	HA*sfc*9 (p=.044); HA*sfc*81 (p=.033)			HA*sfc*9 (p=.009); HA*sfc* 81 (p=.015)	HA*sfc*81 (p=.024); HA*sfc*9 (p=.001); Smc (p=.022)		

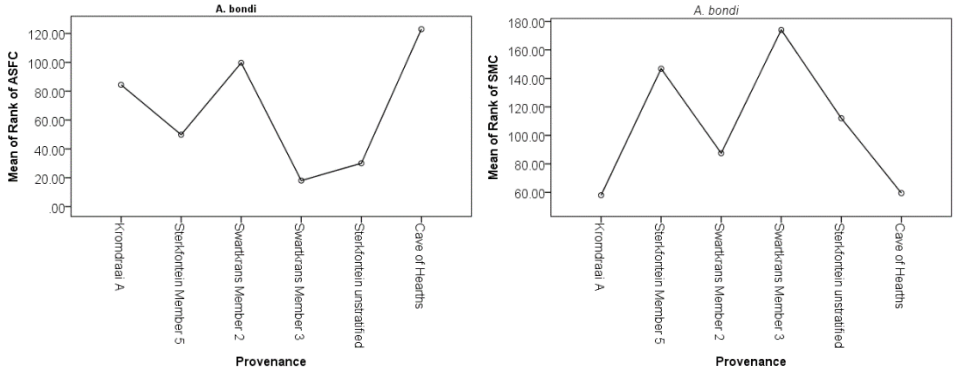


Figure 9.11: Mean ranks for Asfc (left) and Smc (right) for A. bondi through time (by provenance along the Y axis from the oldest deposits on the left, to the youngest deposits on the right) to show the general trend through time. Values are not indicative of variables, only the trend line is of importance.

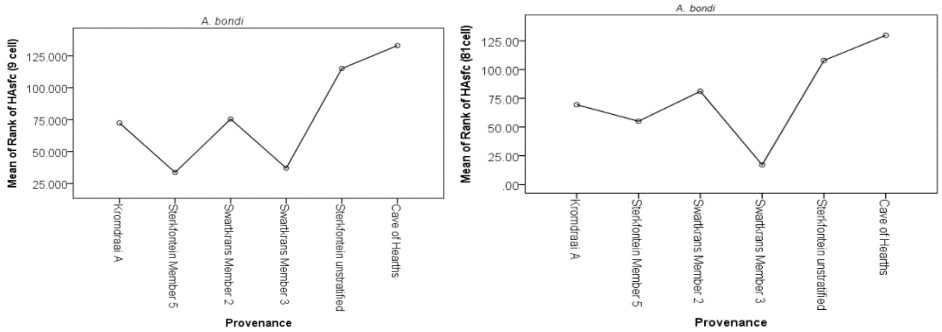


Figure 9. 12: Mean ranks of heterogeneity of dental microwear scarring (HAsfc) for A. bondi through time (provenance) along the Y axis, at differing scales (9cell (left) and 81cell (right)) to show the general trend through time. Values are not indicative of variables, only the trend line is of importance.

Only Swartkrans Member 2 showed significant differences in microwear variable HAsfc (9cell) between *Antidorcas* species (p=0.031). This difference in heterogeneity could lend support to some degree of increased habitat heterogeneity in Swartkrans Member 2. *A. bondi* shows significantly more complex surface wear (Asfc) in Swartkrans Member 2 (mean=2.34µm) than in the earlier, Sterkfontein Member 5 (mean=5.91µm) deposits.

To examine the extent to which individual animal preference may be impacting upon the mean signal, a selection of individuals that have been analysed on an individual animal basis were included. These individuals were the 'potential *Antidorcas australis'* individuals detailed in chapter 4 and analysed in chapter 6, used here as a convenient subset from which to test individual animal DMTA signals. The difference found for Swartkrans Member 2 was between *A. marsupialis* and *Antidorcas* sp. (p=0.017); *A. marsupialis* and '*A. australis*' (p=0.044); *A. bondi* and *Antidorcas* sp. (p=0.036).

Although '*A. australis'* appears to group here, when considering these specimens as individuals (rather than the collective mean values), there is considerable variability and overlap between fossil *A. marsupialis* and '*A. australis'*. Moreover, only one (and at only one scale) of many microwear variables shows any significant difference. This suggests perhaps a population (with the possibility of no temporal overlap), dietary difference within the assemblage at Swartkrans Member 2, rather than a major dietary indicator warranting

the need to revisit species identification. The range of variation shown here is reflective of '*A. australis*' consisting of a combination of the other fossil *Antidorcas* species, as outlined in chapter 6.

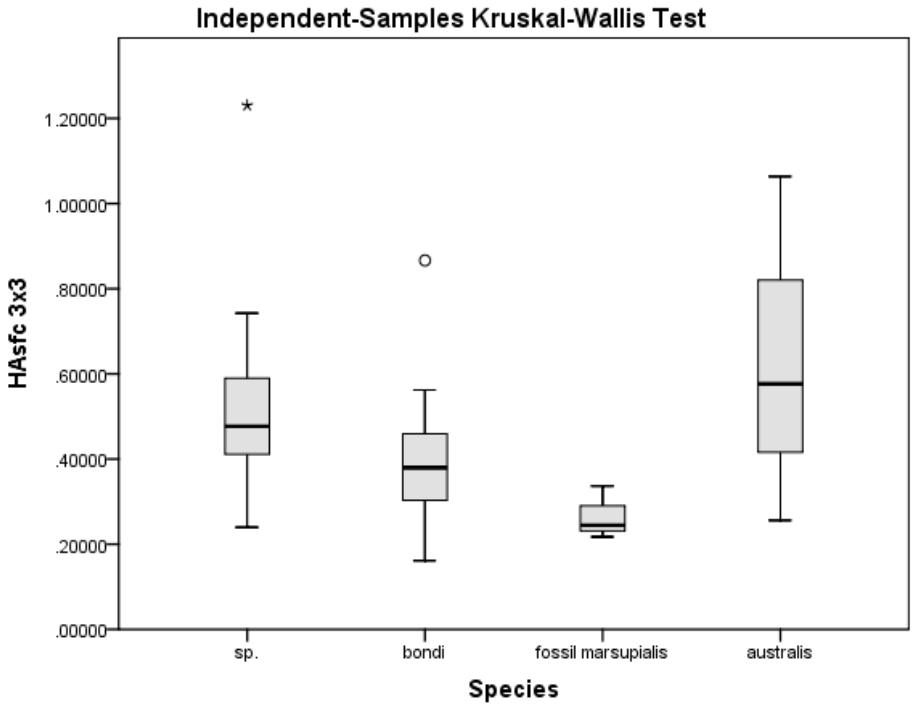
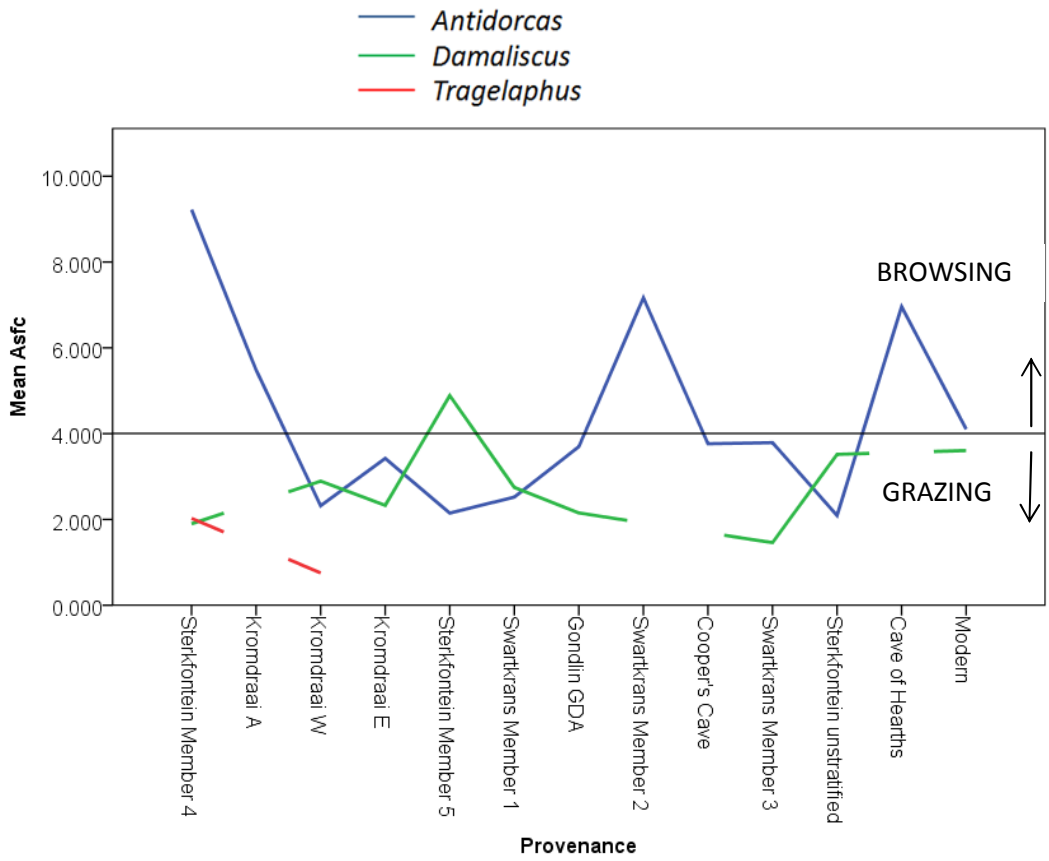
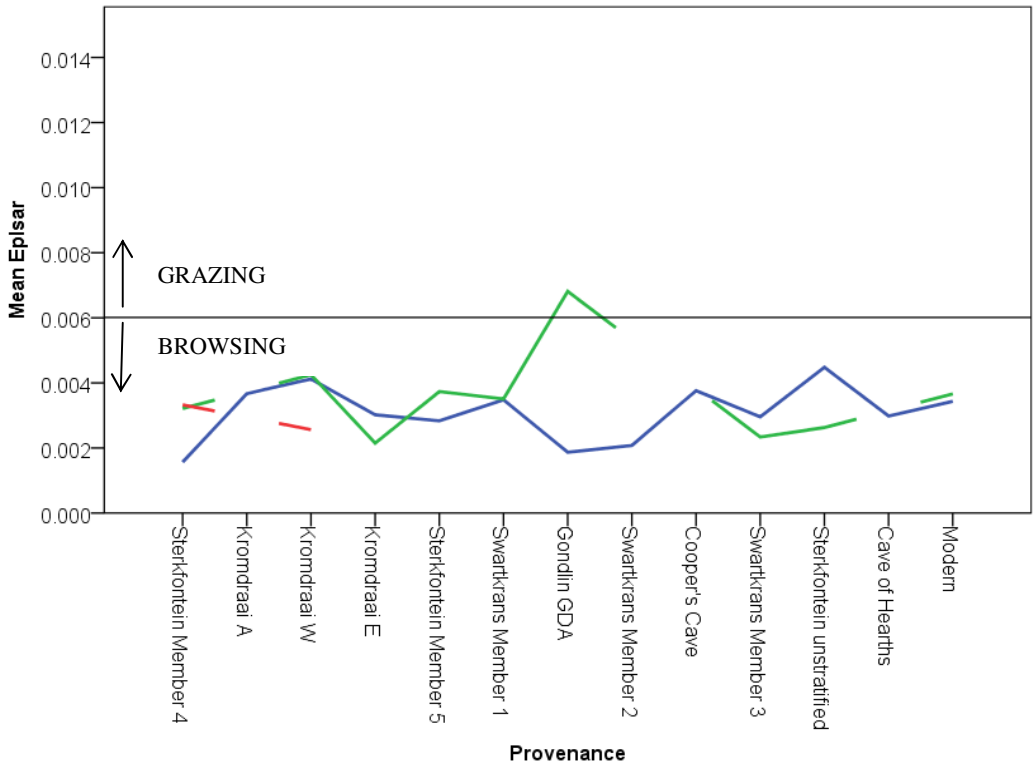


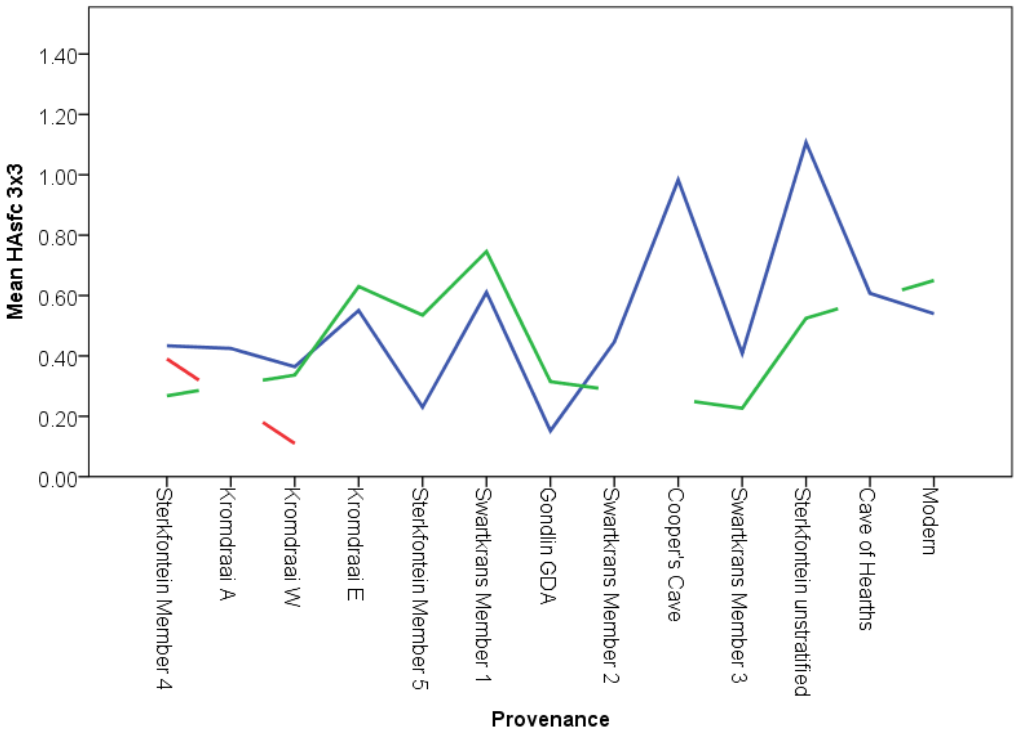
Figure 9.13: Box and whisker plot showing the range of variation for heterogeneity (HAsfc 3x3; 9 cell) for Antidorcas species present in Swartkrans Member 2. Although fossil A. marsupialis has a very small range, it falls within the range of 'A. australis'. 'A. australis' overlaps in range with all other Antidorcas species present.

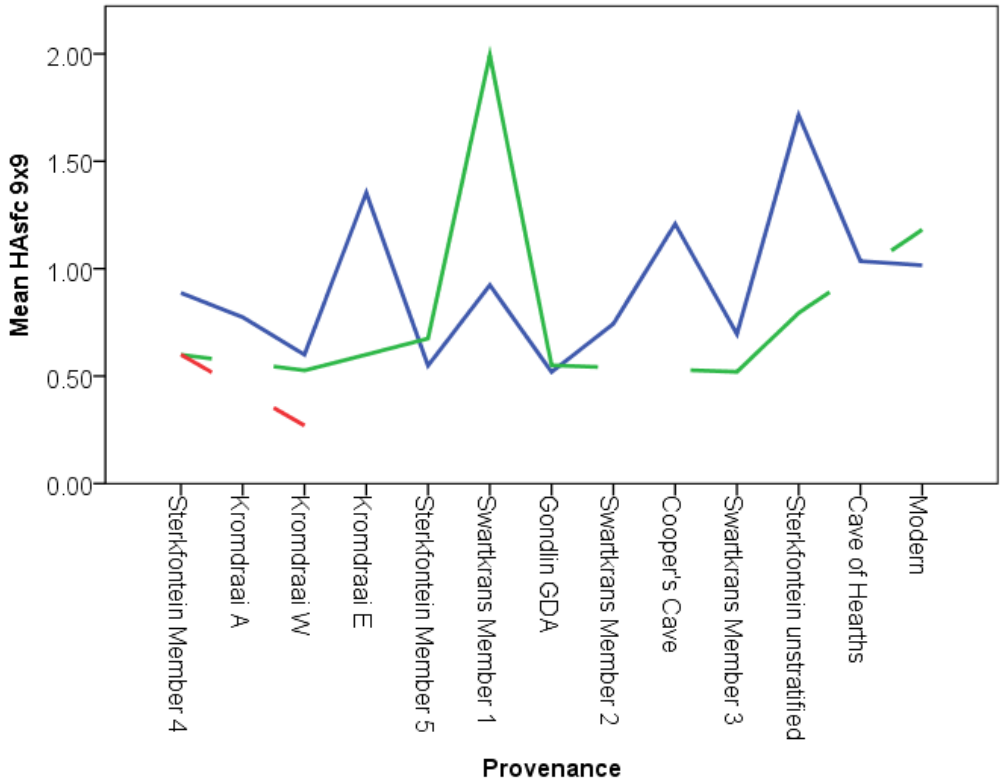
Comparison to Supplementary Species

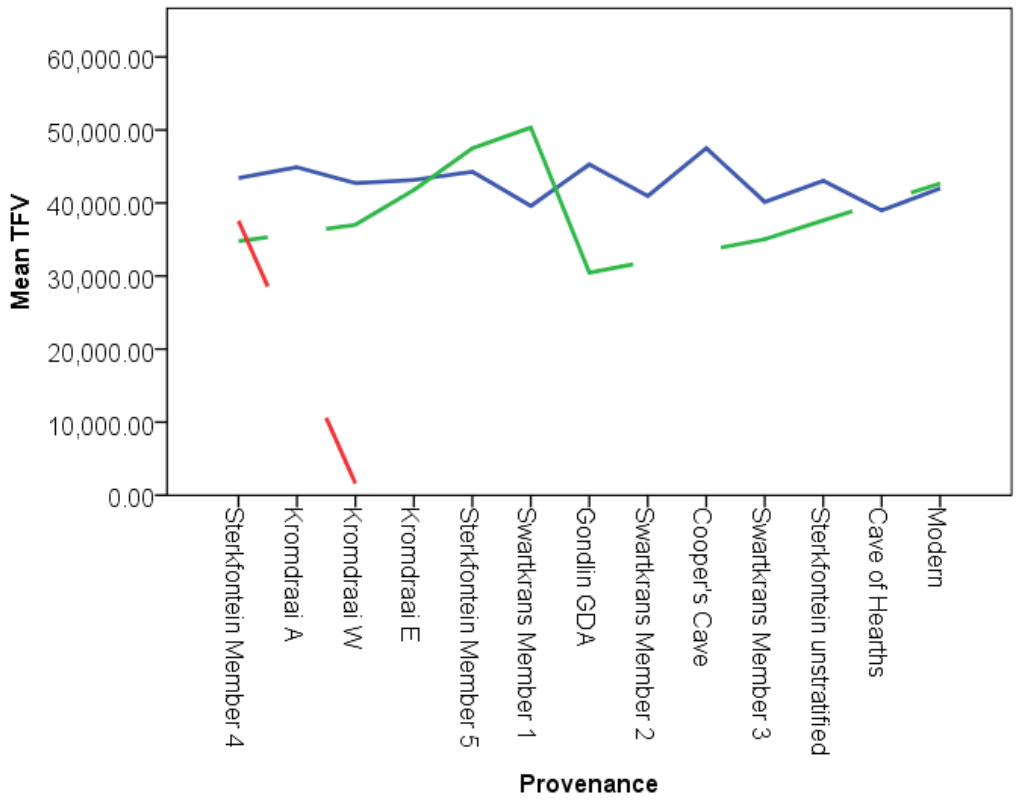
Supplementary fossil species were subject to DMTA for comparative purposes with the *Antidorcas* specimens. Believed grazers, *Damaliscus* (*pygragus*) and browsers, *Tragelaphus* (*strepsiceros*) were used to establish the expected grazing and browsing parameters for each deposit (e.g. Lee-Thorp et al. 1994; Luyt 2001). The results for these supplementary species, compared to results for *Antidorcas*, are considered here.


Antidorcas
Damaliscus
Tragelaphus
Mean Asfc
10.000
8.000
6.000
4.000
2.000
0.000
BROWSING
GRAZING
Sterkfontein Member 4
Kromdraai A
Kromdraai W
Kromdraai E
Sterkfontein Member 5
Swartkrans Member 1
Gondlin GDA
Swartkrans Member 2
Cooper's Cave
Swartkrans Member 3
Sterkfontein unstratified
Cave of Hearths
Modern
Provenance


Mean Eplsar
0.014
0.012
0.010
0.008
0.006
0.004
0.002
0.000
GRAZING
BROWSING
Sterkfontein Member 4
Kromdraai A
Kromdraai W
Kromdraai E
Sterkfontein Member 5
Swartkrans Member 1
Gondlin GDA
Swartkrans Member 2
Cooper's Cave
Swartkrans Member 3
Sterkfontein unstratified
Cave of Hearths
Modern
Provenance


Mean HAsfc 3x3
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
Sterkfontein Member 4
Kromdraai A
Kromdraai W
Kromdraai E
Sterkfontein Member 5
Swartkrans Member 1
Gondlin GDA
Swartkrans Member 2
Cooper's Cave
Swartkrans Member 3
Sterkfontein unstratified
Cave of Hearths
Modern
Provenance


Mean HAsfc 9x9
2.00
1.50
1.00
0.50
0.00
Sterkfontein Member 4
Kromdraai A
Kromdraai W
Kromdraai E
Sterkfontein Member 5
Swartkrans Member 1
Gondlin GDA
Swartkrans Member 2
Cooper's Cave
Swartkrans Member 3
Sterkfontein unstratified
Cave of Hearths
Modern
Provenance



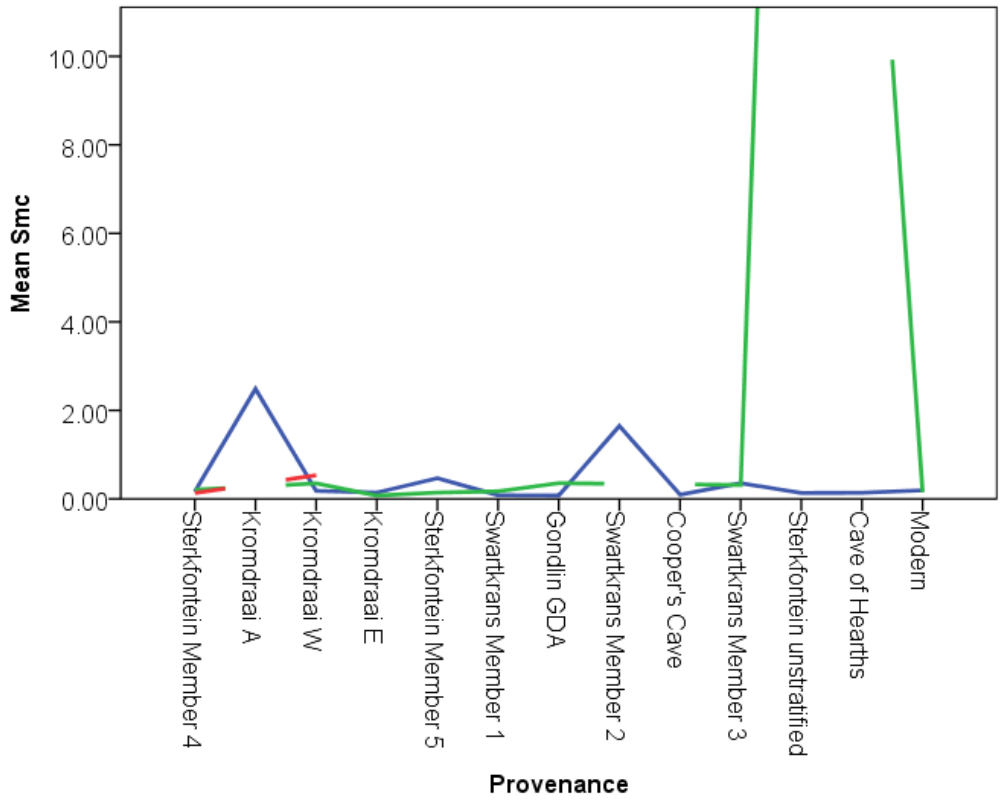


Figure 9.14: A series of line graphs showing mean dental facet surface texture variables for Antidorcas, Damaliscus and Tragelaphus (where present) through time (relative chronology as detailed in chapter 2, Table 2.2). Gaps in the line show an absence of data collected. The horizontal lines delineate grazing (Asfc values below the line; epLsar above the line) from browsing (Asfc values above the line; epLsar below the line) dominance. Smc for Sterkfontein unstratified is much higher than the stratified deposits (c. 40 µm) and is not included to ensure the detail of the stratified deposits is shown. HAsfc 3x3 corresponds to 9cell; 9x9 to 81 cell.

Comparative *Antidorcas* palaeoecology

Fossil *Antidorcas* species were assessed against modern species of known diet to establish the dietary indicators from a range of species of differing dietary niches. Both fossil (all species) and modern *Antidorcas* anisotropy (epLsar) values differ significantly from the modern grazing species; *Syncerus caffer* and *Alcelaphus buselaphus*.

Comparison of *Antidorcas* with other species through time

Unfortunately, small sample sizes for each site prevented these patterns being explored for *Tragelaphus* (as the believed browsing supplementary species) through time. Sterkfontein Member 4 appears more heterogeneous in dietary patterns, and by inference, in vegetation available for consumption. From the graph (Figure 9.14) of dental facet surface complexity (Asfc), *Antidorcas* shows extreme complexity, indicative of low occlusal surface abrasion and a dominance of browsing, as may be expected for Sterkfontein Member 4 (c. 2.8-2.5 Ma) and for periods where *A. recki* dominates. However, *Damaliscus* shows a faithful grazing signal (primarily via low complexity), indicating the presence of at least some grassland habitats. The opposite occurs in Sterkfontein Member 5 (c. 1.7 Ma), whereby *Antidorcas* has a stronger grazing signal than *Damaliscus* but both still show an inclusion of grazing in the diet (relatively low surface complexity, Asfc). This could indicate palaeoenvironmental change through time (increase in grasslands and homogeneity of habitats from Sterkfontein Member 4 to Member 5) in isolation or with the addition of increased biotic competition. All species show low anisotropy (epLsar) throughout this temporal range. Although epLsar values are variable through time, they remain within the mixed-feeding / browsing range. Only *Damaliscus* in Gondolin (GDA) displays a typical grazing epLsar value.

Table 9.6: Pairwise comparison of species DMTA values. Significant differences are showen, these significant differences were obtained via an ANOVA and post-hoc Fishers LSD (above the diagonal) and Tukey's HSD (below the diagonal). P values are given in brackets next to the significant variable. Abbreviations used for taxa are as follows: Ar=A. recki, Ab=A.bondi, Am=A.marsupialis, Dp=D. pygargus, Abs=A.buselaphus, Sc=S.caffer, Gc=G.camelopardalis, Cs=C. sylvicultor.

		Fossil			**Modern**					
		Ar	**A*b***	***Am***	***Am***	***Dp***	***Abs***	***Sc***	***Gc***	***Cs***
Fossil	***Ar***						Asfc(<.000); epLsar(<.000); Smc(.001)	Asfc(<.000); epLsar(.003); Smc(.001)	Asfc(.024); Tfv(.007)	Smc(.001)
	Ab						Asfc(<.000); epLsar(<.000); Smc(<.000)	Asfc(<.000); epLsar(.001); Smc(<.000)	Asfc(.038)	Smc(<.000)
	Am						Asfc(<.000); epLsar(<.000); Smc(<.000)	Asfc(<.000); epLsar(.007); Smc(<.000)	Smc(.049)	Smc(<.000)
Modern	***Am***	Asfc(.025)	Asfc(.046)	HAsfc81(.029)			Asfc(.003); epLsar(.002); HAsfc9(.050); HAsfc81(.010); Smc(<.000)	Asfc(.001); HAsfc9(.016); HAsfc81(.001); Smc(<.000)		Smc(<.000)
	Dp	Asfc(.008); Tfv(.047)	Asfc(.014)	Smc(.049)			epLsar(.017); Smc(.009)	Asfc (.020); Smc(.025)		Smc(.010)
	Abs	Asfc(<.000); epLsar(<.000); HAsfc81(.018); Smc(<.000)	Asfc(<.000); epLsar(<.000); HAsfc9(.022); HAsfc81(.006); Smc(<.000)	Asfc(<.000);epLsar(<.000); HAsfc9(.037); Smc(<.000)	Asfc(<.000); epLsar(<.000); HAsfc9(<.000); HAsfc81(<.000); Smc(<.000)	Asfc(.001);epLsar(.017); HAsfc9(.007); HAsfc81(.010); Smc(<.000)			Tfv(.016)	Asfc(.006); epLsar(.001)

		Fossil			Modern					
		Ar	**A*b***	***Am***	***Am***	***Dp***	***Abs***	***Sc***	***Gc***	***Cs***
	Sc	Asfc(<.000); epLsar(<.000); HAsfc81(.005); Tfv(.014); Smc(<.000)	Asfc(<.000); epLsar(<.000); HAsfc9(.012); HAsfc81(.001); Smc(<.000)	Asfc(<.000); epLsar(<.001); HAsfc9(.025); HAsfc81(.036); Smc(<.000)	Asfc(<.000); epLsar(.002); HAsfc9(<.000); HAsfc81(<.000); Smc(<.000)	Asfc(<.000); epLsar(.010); HAsfc9(.004); HAsfc81(.002); Smc(<.000)	Tfv(.030)			Asfc (.002)
	Gc	Asfc(<.000); Tfv(<.000); Smc(.008)	Asfc(<.000); HAsfc81(.030); Tfv(.001); Smc(.001)	Asfc(.007); Tfv(.007); Smc(<.000)	Asfc(.034); epLsar(.003); HAsfc9(.011); HAsfc81(.002); Tfv(.001)	epLsar(.002); HAsfc81(.039); Tfv(.012); Smc(.048)	epLsar(<.000); Tfv(<.000)	epLsar(<.000); Tfv(.032)		
	Cs	Tfv(.001); Smc(<.000)	HAsfc81(.032); Tfv(.010); Smc(<.000)	Smc(<.000)	HAsfc9(.010); HAsfc81(.001); Tfv(.019); Smc(<.000)	HAsfc81(.046); Smc(<.000)	Asfc(<.000); epLsar(<000) ; Tfv(.002)	Asfc(<.000); epLsar(.001)	Asfc(.030); epLsar (.021)	

9.3 DISCUSSION

It is important to consider the individual diets rather than simply the mean for any given member or species. This is particularly true for mixed-feeding herbivores, such as the springbok. Although a 'mixed-feeding' signal may be inferred from comparing averaged values and signals, individuals within each population can be specialized grazers/browsers on an individual animal scale, but making them a mixed feeder at the species level (e.g. Lehmann et al. 2015). *Antidorcas*, as a mixed-feeding taxon, is nevertheless, an appropriate bioproxy from which to track palaeovegetation changes (e.g. Berlioz et al. 2018).

9.3.1 *Antidorcas* palaeoecology

DMTA variables inform on the palaeodietary signals of fossil *Antidorcas*, establishing what these *Antidorcas* ate, at least for the last few days-months prior to death.

A. recki

A. recki is evidenced to have a largely faithful browsing-dominated diet but showed a shift from browsing during Sterkfontein Member 4 to significantly increased inclusion of grass, to a grazing level of surface complexity, in Kromdraai W. All other Members show *A. recki* to be predominantly browsing.

A. bondi

A. bondi displays more mixed-feeding and browsing microscopic wear throughout this temporal range than may be anticipated based on stable carbon isotope analysis from Brink & Lee-Thorp (1992). However, considering what DMTA results can add to the debate on *A. bondi* grazing succession, if *A. bondi* fed close to the ground, grazing on the smallest grass shoots, HAsfc might be expected to be elevated, along with higher than anticipated epsLar values due to the inclusion of exogenous grit associated with ground-level feeding. It is possible that these increased 'browsing' signals are actually due to an inclusion of grit. In spite of testing of the impact of dust and other exogenous particle influence on microwear signals having shown diet is the dominant signal obtained (e.g. Merceron et al. 2016), it is possible grit inclusion is visible here. Further, feeding on fresh grasses is less likely to leave scarring than mature grasses (Massey et al. 2008). Therefore, *A. bondi* feeding on new shoots preferentially is less likely to leave a trace of this dietary practice on its dentition, reducing the lasting grazing signal. Untangling this possibility from one of an *A. bondi* dietary shift prior to death (from grazing in the earlier years as evidenced by stable carbon isotope analysis, to increased inclusion of browse via DMTA) is complicated.

As Merceron et al. (2016) show, diet is the prevalent signal achievable via DMTA, with exogenous particles having far less impact on the DMTA variables in comparison. Therefore, to assess the reasoning behind *A. bondi*'s apparent increased browse component of diet versus grit consumption, DMTA variables of Tfv and Smc are useful. A predominantly grazing diet with some influence of exogenous particles is likely to have the wear concentrated at a much finer scale (Smc) than a typical browsing wear pattern may exhibit. Smc and Tfv were not significantly different from either the mixed-feeding modern *A. marsupialis* or the browsing *A. recki* when combined as a species through time or between species for any individual member. Significant differences were however apparent

for Smc (scale of maximum complexity) for *A. bondi* between Sterkfontein Member 5 (coarser scale) and Kromdraai A, and Cave of Hearths (finer scale) (and a weaker difference between Sterkfontein Member 5 and Swartkrans Member 2 (finer scale), and between Swartkrans Member 3 (coarse scale) and Cave of Hearths). This suggests that *A. bondi* from Sterkfontein Member 5 (and Swartkrans Member 3) included more browse in its diet, or at least vegetation which produced different sized pit-scarring. Coarser scale complexity is likely to be more indicative of larger, more irregular shaped particle-induced pitting.

Modern *Antidorcas marsupialis* differs significantly in Smc values from *Syncerus caffer* (African buffalo; grazes on long grass), *Alcelaphus buselaphus* (hartebeest; grazes on all parts of the grass) and *Cephalophus sylvicultor* (yellow-backed duiker; fruit browser) (Kingdon 1997). Therefore, one might expect *A. bondi* to differ significantly from *A. recki* if the causality of the increased 'browsing' signal for *A. bondi* was due to diet. However, *Damaliscus pygargus* (bontebok; diurnal grazers consuming mainly short grasses) also differs significantly from the same species as *A. marsupialis*. For Tfv values, only the leaf-browsing *Giraffa camelopardalis* (giraffe) differ significantly from the mixed-feeding *A. marsupialis*. These findings for modern species of known dietary intake may support using Smc values to identify the impact of exogenous particles on overall DMTA. Collectively as a species, *A. bondi* differs significantly from the same species as the modern mixed-feeding *A. marsupialis*. Additionally, *A. recki* and *A. bondi* differ significantly from the same modern (grazing) species (Table 9.6). This evidence suggests on balance, that *A. bondi*'s DMTA more accurately reflects mixed feeding to browsing at the end of life, rather than the inclusion of exogenous grit *in a graze-dominated* diet.

The possibility exists that *A. bondi* still consumed grasses but perhaps shifted to C_3 grasses that leave finer imprints on the enamel surface that therefore were more vulnerable to overwriting (Solounias and Semprebon 2002).

A. marsupialis

DMTA shows fossil *A. marsupialis* to have a browse-dominated mixed feeding diet throughout. *A. marsupialis* shows no directional change through time and no evidence of significantly changing its diet between any particular time period (member).

9.3.2 Dietary abrasion

Schulz et al. (2013) suggest the importance of an abrasive diet in the microwear patterning evident on dental surfaces. Their experiment on rabbits showed that an abrasive diet, linked to hypsodonty (as also shown to be correlated to dietary abrasiveness) is more susceptible to overprinting, making microwear signals from animals with a highly abrasive diet representative of a shorter time period. Higher heterogeneity would suggest lower levels of overwriting as the surface isn't being routinely abraded, which would also show up in Tfv values. An abrasive diet is more likely to create a planar surface (lower Tfv values).

The need for the adaptation of the methodological approach of DMTA software analysis to subtract the polynomical surface implies a highly abrasive diet for both the mixed-feeding

A. marsupialis and *A. bondi*. *A. recki* did not appear to share this issue, and by inference, did not have such an abrasive diet.

A less abrasive diet is likely to result in slower overwriting of previous microscopic wear scars, thereby increasing the complexity of the enamel surface texture. Lower abrasion may be due in part to fewer exogenous particles impacted on the enamel surfaces, and not always due to ingested food particles, i.e. reduced abrasive grass silicas, and therefore, abrasion could perhaps falsely emphasise the browsing component on the diet. As discussed in previous chapters, *Antidorcas*, particularly *Antidorcas bondi*, appear to have had a relatively abrasive diet. Although this abrasion may be due, at least in part, to an inclusion of dietary grasses, the browsing scarring is likely to be an overstated dietary constituent from microwear variables, in contrast to the finer grazing striations that are more vulnerable to overwriting. Thus, due to the high level of abrasion, the grazing signal is more likely to be consistently abraded, with deeper browsing-induced pitting skewing the microwear signal towards a mixed-feeding or browsing diet. Low Asfc, wth low HAsfc can also be indicative of leaf browsing. This is taken further in the subsequent 'Multi-Method' chapter.

9.3.3 DMTA as an indicator of palaeoenvironments through time

Whilst bearing in mind individual specialisations and preferences, mean signals and ranges compared between members can give an idea of the prevailing vegetation shifts through time. As well as an idea of the dietary variability through time, which in itself can give insight into the vegetation type abundance in any given time period. More variation, coupled with greater species abundance, may indicate greater variability in vegetation available.

In addition to dietary information, DMTA signals can highlight palaeoenvironmental conditions. Exogenous dust particles (e.g. an increase in eolian dust) or grit taken in with the food particles will inevitably produce similar scarring on the enamel surface (e.g. Wood 2013), although the impact of exogenous particles, such as dust, appears to be far less than from the intrinsic food particles (Merceron et al. 2016).

DMTA variability for Sterkfontein Member 5 and Swartkrans Member 2 perhaps indicate a more changeable palaeoenvironment, with mosaic habitats and probable increased seasonality (indicated via individual animal assessment and the dietary variability prevalent for an individual). Higher heterogeneity (HAsfc) suggests a more variable diet (e.g. Hofman-Kamińska et al. 2018), yet Swartrkrans Member 2, and particularly Sterkfontein Member 5 *Antidorcas*, show more homogenous dietary wear patters. Kromdraai E and Sterkfontein unstratified *Antidorcas* specimens show the greatest mean heterogeneity of diet.

However, when considering individuals within each assemblage, many of those from Swartkrans Member 2 and Sterkfontein Member 5 have high heterogeneity and some high homogeneity. Thereby supporting the suggestion of these members being deposited during a period of palaeoenvironmental instability and/ or high habitat heterogeneity. This diametric differentiation is more prevalent for Swartkrans Member 2. This may be an

artefact of sample size or suggest the palaeoenvironmental/ palaeohabitat variability in Swartkrans Member 2 was stronger than for Sterkfontein Member 5.

If the browse-dominated signal shown here incorporates the inclusion of CAM plants (see glossary and chapter 4) in the diet, this could provide a key insight into palaeoenvironmental conditions. Modern springbok are known to consume succulents (typically CAM) for their high moisture content. CAM plants, as an anti-herbivory defence, invest heavily in features such as thorns (e.g. acacia plants). As such, CAM plant consumption may be expected to manifest on the dental enamel in a similar way to a browsing diet. Yet the inclusion of CAM would showcase increased aridity levels as they typically inhabit and thrive under arid conditions. Untangling the CAM signal from the normal browse signal is an avenue for future research.

9.4 SUMMARY

- *Antidorcas* species showed differential change through time. *Antidorcas recki* showed a shift from browsing during Sterkfontein Member 4 to significantly increased inclusion of grass, to a grazing level of surface complexity, in Kromdraai W. All other members show *A. recki* to be predominantly browsing. *Antidorcas bondi* has unexpected mixed-feeding to browsing microwear patterns throughout the temporal range, significantly, from the grazing level of enamel surface complexity in Sterkfontein Member 5 compared to a browsing-range of complexity in Swartkrans Member 2.
- *Antidorcas bondi*'s unexpected mixed-feeding to browsing diet shown may either indicate an increase in browse in these members, or shortly before death. However, it is possible that this could be a false indicator due to the high level of dietary abrasiveness, skewing the signal in favour of longer-lasting microscopic scars left by browse particles (varying depth and size of pits from seeds/twigs/leaves), compared to the fine scratches imparted by mastication on grasses which are more-readily abraded. Alternatively, exogenous grit from being a low-level feeder could mimic or exaggerate more browse-dominated dietary signals.
- No major dietary change through time was evident for *Antidorcas marsupialis*.
- A temporally variable mosaic habitat landscape is inferred from *Antidorcas* DMTA variables, with a shift from predominantly browsing from Sterkfontein Member 4 towards more mixed-feeding habits of *Antidorcas*. Swartkrans Member 2 (Asfc and epLsar) and perhaps Cave of Hearths (Asfc) show significantly increased browsing signals compared to other temporal periods.
- DMTA variability for Sterkfontein Member 5 and Swartkrans Member 2 perhaps indicate a more changeable palaeoenvironment, with mosaic habitats and possible increased seasonality.
- Although individual animals within each species had varying diets, taking the overall species signal, all *Antidorcas* were mixed-feeders/ browsers from the late Plio-early Pleistocene in South Africa.

CHAPTER 10

Stable Isotope Analysis

Landscape vegetation and plant growth is dictated primarily by climate and regional topography (Vogel 1978). The isotopic composition of the plants that animals consume determines the isotopic signature found in the animal's bones or teeth. The type and part of plant ingested dictates the quantity and distribution of these chemical compounds found via isotopic analysis of herbivore dental enamel (DeNiro and Epstein 1978).

Today, most of the South African subcontinent, including the Cradle of Humankind, falls into the summer rainfall zone, with C_4 taxa dominating (Vogel et al. 1978). In order to understand palaeoenvironmental factors, such as the vegetation cover, aridity and palaeodiets, isotopic analysis (carbon and oxygen) is conducted, using *Antidorcas* dental enamel.

This chapter introduces the use of stable isotope analysis (carbon and oxygen) as a method for inferring palaeoenvironmental conditions, before being applied to a selection of the *Antidorcas* dental enamel samples. The dental enamel sampled here (chapter 4, section 4.6.4; this chapter, section 10.2) is compared to stable isotope values of *Antidorcas* (and a few other supplementary species where appropriate) dental enamel from published sources, as detailed below (and see Appendix A8).

10.1. BACKGROUND

Stable isotopes preserved within the teeth and bones of animals can be used to infer palaeovegetation cover through tracing the animals' diet (Vogel 1978). At the base of the food chain, the growth of plants is directly influenced by the climate (temperature and hydrological influences) and topography (altitude, soil matrix and geochemistry) of the area (Vogel 1978). Plants contain differing levels of certain stable isotopes, according to the way they fractionate chemical compounds (Vogel 1983; Cerling et al. 1997). The isotopic signatures of the plants are passed on through the trophic levels upon consumption. In turn, these isotopes are integrated into the animal's body tissues as they consume and digest these plants (Pollard & Heron 2008).

The distribution and concentration of these stable isotopes (based on their mass-to-charge ratio as preserved within the animals' bone and dental enamel in teeth) can be measured using mass spectrometry (e.g. Hopley et al. 2006; Bernard et al. 2009; Lehmann et al. 2016). Enamel is used primarily to look for the isotopic signature largely due to its longevity, being sufficiently hard a substance to resist many diagenetic processes (Wang and Cerling 1994; Luyt 2001) that other skeletal material is more susceptible to.

Carbon and oxygen isotopes are often studied together for dietary reconstructions as they are directly related to the type of plants and the meteoric water ingested by individuals. These isotope values are therefore, indicative of the vegetation cover, available habitat types and aridity levels of their inhabited landscape. For the purposes of palaeoenvironmental reconstructions, carbon and oxygen isotopes are often used and used in conjunction with use-wear analysis (microwear/mesowear) to provide a long-term picture of diet throughout the animal's lifetime (Hopley et al. 2006; Louys et al. 2012).

Carbon isotopes are suggestive of the relative availability of C_3/C_4/CAM plants. The relative percentage of C_3/C_4-plant-consuming animals provides information about the local environment. Thereby, indicating how open/closed an environment was.

As alluded to in the previous chapters, vegetation changes only go so far in informing us of the climate and any climatic changes. Oxygen isotopes, however, are indicative of the moisture content of an area, thus should be more directly related to climate. This is especially true when methods are then used in conjunction with one another to indicate vegetation and hydrological trends.

Known isotope signals (published data trend)

CARBON ISOTOPES

$\delta^{13}C$ values of C3 plants globally range from ~-31.7‰ to -23.1‰ (Kohn 2010) and C4 plants between ~-14.0‰ and -10.0‰ (Hattersley 1982). A dietary enrichment of +14.1‰ of $\delta^{13}C$ values exists between the plants ingested by large (>6kg) herbivores and that preserved in their enamel (Cerling & Harris 1999) see (chapter 4). The browsing (C_3-dominated) and grazing (C_4-dominated) dietary categories are indicative of individuals with diets dominated by C_3 and C_4 vegetation respectively. Pure browsing taxa have $\delta^{13}C$ values around -12 to -14‰, whereas pure grazers have values between around 0 to +2‰ (Lee-Thorp et al. 2000) see Figure 4.22. Based on the ranges of $\delta^{13}C$ data for modern herbivores in South Africa (Sponheimer et al., 2003), dietary carbon isotope values are taken as follows: $\delta^{13}C$ enamel values below -9‰ indicate C_3 dietary dominance (browsing); above -3‰ indicate C_4 dietary dominance (grazing) with values between -9‰ and -3‰ being taken as mixed feeders (Sponheimer et al. 2003; Lee-Thorp et al. 2007). Browsing to mixed-feeding $\delta^{13}C$ values typically arise for modern springbok, which are considered to be seasonal mixed-feeders, consuming more browse in winter and grazing in summer (Kingdon 1997; Gagnon & Chew 2000).

Previous studies using *Antidorcas*, suggest that *A.marsupialis* should be depleted in $\delta^{13}C$, as a mixed feeder, whilst, as a believed grazing springbok, *A. bondi* would be expected to have more enriched values nearer 0% (Brink & Lee-Thorp 1992). In contrast, *A. recki* would be expected to show levels depleted in $\delta^{13}C$ (e.g. Lee-Thorp et al. 2007).

Little has been published on the impact of CAM plants but it is likely that an inclusion of CAM plants in *Antidorcas* diet will give an inflated range (more enriched in $\delta^{13}C$) of $\delta^{13}C$ signals (Wang et al. 2008), in a similar way to that of C_4 plants, as discussed above.

OXYGEN ISOTOPES

Research into Plio-Pleistocene environments has often used $\delta^{18}O$ isotope values to indicate aridity levels. For instance, a shift from Sterkfontein Member 4, to more positive $\delta^{18}O$ values for Sterkfontein Member 5 lends further support for a landscape with more open environments (e.g. Luyt 2001). The published data of $\delta^{18}O$ isotope values for South African sites is considered here, and coupled with the data obtained from this study alongside the carbon isotope values, to indicate South African Plio-Pleistocene environmental trends and variability.

For *Antidorcas*, increased sweating due to a lack of tree cover and shade (Luyt 2001) associated with a spread of open grassland habitats would presumably add to the isotopic values found. Indeed, Lehmann et al. (2016) concluded that beyond regional aridity increase and global cooling, other factors, such as spring-fed local areas must have played a part in the increased $\delta^{18}O$ values witnessed across the early Pliocene to mid-Pleistocene, i.e. the animal's individual or species differential behavioural response to changing environments must be considered. Although the overall increasing aridity trend prevails, buffers such as thermoregulatory adaptation and water resource usage will differ species to species and knowledge of their likely palaeoecology will aid in inferring their isotopic signatures. Luyt's (2017) study on African mammal light isotope signatures highlighted crucial differences in values for the mixed-feeding modern *Antidorcas marsupialis*, depending upon the vegetation biome inhabited.

Table 10.1: Modern Antidorcas marsupialis carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope value differences depending on vegetation biome inhabited. All values given to 1 decimal place. Values from Luyt (2017).

Biome*	Isotope (PDB) (‰)	N	Median	Minimum	Maximum	Mean	S.D.
Nama Karoo	$\delta^{13}C$	23	-11.7	-14.5	-7.8	-11.4	1.5
	$\delta^{18}O$		4.8	2.6	10.1	4.9	1.5
Savanna	$\delta^{13}C$	4	-10.8	-11.9	-10.1	-10.9	0.7
	$\delta^{18}O$		4.4	3.3	5.2	4.3	0.8
Succulent Karoo	$\delta^{13}C$	14	-11.9	-16.6	-7.0	-11.7	2.1
	$\delta^{18}O$		4.9	-0.5	6.1	4.0	2.0

*Succulent karoo is a semi-desert biome with a high diversity of succulent plants and low but seasonal mean annual precipitation, around 170mm (Mucina and Rutherford 2006). Nama karoo is very arid with dwarf open scrubland, and a mean annual precipitation of between 40-400mm falling mainly in the summer months (Mucina and Rutherford 2006). Savanna is characterised by a hot climate with wet summers and warm, dry winters (Scholes 1997) supporting tropical vegetation with a mix of woody plants and grasses. Savanna is less arid than the karoo biomes.

It is an avenue for future work to apply algorithms to the data to offset these values to make them exactly comparable to fossil *Antidorcas* values. However, all modern *Antidorcas* sampled in Luyt's (2017) study show mixed-feeding to browsing preference with relatively enriched $\delta^{18}O$ values, indicative of inhabiting semi-arid to arid environments.

10.2 RESULTS

Table 10.2: Modern isotope values (δ13C ‰ and δ18O ‰) for species of known diet, for comparison with fossil taxa.

Species	$\delta^{13}C$ (‰) PDB	$\delta^{18}O$ (‰) SMOW	$\delta^{18}O$ (‰) PDB	Diet	Reference
A. marsupialis	-18.10	N/A	N/A	Mixed Browser	Vogel 1978
A. marsupialis	-10.10	N/A	N/A	Mixed Browser	Sponheimer et al. 2003
A. marsupialis	N/A	37.2	6.15	Mixed	Sponheimer & Lee-Thorp 1999
A. melampus	-3.3±3.3	34.5±1.2	3.52	Mixed	Sponheimer & Lee-Thorp 2001
D. pygargus	0.5	x	x	Grazer	Sponheimer et al. 2003
D. pygargus	-2.7	30.14	-0.7	Grazer	Luyt 2017
C. taurinus	+2.8±0.5	30.7±1.2	-0.16	Grazer	Sponheimer & Lee-Thorp 2001
D. lunatus	+2.3±0.6	32.0±0.9	1.10	Grazer	Sponheimer & Lee-Thorp 2001
K. elliprymnus	+1.6±1.1	29.7±1.6	-1.13	Grazer (water-dependent)	Sponheimer & Lee-Thorp 2001
T. strepsiceros	-13.0	N/A	N/A	Browser	Sponheimer et al. 2003
T. strepsiceros	-12.7	35.50	4.5	Browesr	Luyt 2017
G. camelopardalis	-16.8±0.6	29.4±2.1	-1.42	Browser	Sponheimer & Lee-Thorp 2001

Sample analysed as part of this research

Table 10.3: This study carbon and oxygen ($\delta^{13}C$ (‰) & $\delta^{18}O$ (‰)SMOW) for Swartkrans (SKX) Antidorcas dental enamel. Diet is based on carbon isotope values typical of modern South African herbivores (Sponheimer et al. 2003), where values are close to the boundaries (>-3‰ C_4 consumers and -9‰ C_3 consumers), they are seen to be less catholic in their dietary habits. Those in red highlight the individuals with the highest and lowest $\delta^{13}C$ values for each Member. Diets: 'B'=Browser, 'M'=Mixed feeder, 'G'=Grazer.

Specimen #	Provenance	Species	$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)SMOW	$\delta^{18}O$ (‰) PDB	Diet	Sampling method
SKX10697	SKX M1	*A. marsupialis*	-7.19	+26.24	-4.48	M	Bulk
SKX4842	SKX M1	*A. marsupialis*	-7.01	+31.50	0.62	M	Bulk
SKX10703	SKX M1	*A. marsupialis*	-4.66	+43.97	12.72	M	Bulk
SKX11602 A	SKX M1	*A. marsupialis*	-7.45	+29.63	-1.20	M	Serial
SKX11602 B	SKX M1	*A. marsupialis*	-9.19	+31.34	0.46	B	Serial
SKX11602 C	SKX M1	*A. marsupialis*	-9.43	+30.77	-0.09	B	Serial
SKX11602 D	SKX M1	*A. marsupialis*	-9.73	+31.21	0.34	B	Serial
SKX11602 E	SKX M1	*A. marsupialis*	-9.66	+29.73	-1.10	B	Serial

Specimen #	Provenance	Species	$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)SMOW	$\delta^{18}O$ (‰) PDB	Diet	Sampling method
SKX11602F	SKX M1	*A. marsupialis*	-9.85	+31.01	0.14	B	Serial
SKX36545	SKX M3	*A. marsupialis*	-8.11	+29.13	-1.69	M	Bulk
SKX34249X	SKX M3	*A. marsupialis*	-4.10	+36.00	4.98	M	Bulk
SKX34249X (REP)	SKX M3	*A. marsupialis*	-6.24	+34.43	3.46	M	Bulk (repeat)
SKX33839	SKX M3	*A. marsupialis*	-9.08	+30.83	-0.03	B	Bulk
SKX28999	SKX M3	*A. marsupialis*	-5.20	+34.46	3.49	M	Bulk
SKX28008B	SKX M3	*A. marsupialis*	-9.27	+34.60	3.63	B	Serial
SKX28008C	SKX M3	*A. marsupialis*	-8.92	+37.91	6.83	M	Serial
SKX35326	SKX M3	*Antidorcas* sp.	-10.82	+31.29	0.41	B	Bulk
SKX34249A	SKX M3	*Antidorcas* sp.	-8.26	+31.36	0.48	M	Serial
SKX34249B	SKX M3	*Antidorcas* sp.	-7.63	+31.40	0.52	M	Serial
SKX34249C	SKX M3	*Antidorcas* sp.	-7.56	+32.30	1.40	M	Serial
SKX34249D	SKX M3	*Antidorcas* sp.	-8.44	+34.21	3.25	M	Serial
SKX34249E	SKX M3	*Antidorcas* sp.	-7.62	+38.09	7.01	M	Serial
SKX34249F	SKX M3	*Antidorcas* sp.	-7.63	+39.40	8.28	M	Serial
7.5MG ENAMEL	Modern	Bovid	+0.04	+32.58	1.67	G	Standard
13.6MG ENAMEL	Modern	Bovid	-0.96	+31.67	0.78	G	Standard
13.6MG ENAMEL	Modern	Bovid	-0.90	+31.65	0.76	G	Standard

This study results: serial sampling

The carbon isotopes from this select study of *Antidorcas* for Swartkrans Member 1 and 3 show browsing-dominance, with no obvious seasonality in dietary behaviour. However, the oxygen isotopes from the same individuals show a substantial shift (c. 4 per mil ‰). The higher values presumably represent the dry season when increased evapotranspiration leads to higher leaf $\delta^{18}O$ values. As *Antidorcas* (at least, modern *Antidorcas*) obtain the majority of their water from leaf water rather than by drinking standing water, these $\delta^{18}O$ values are most likely reflective of browse consumed. The two individuals analysed by serial sampling show consistency with animals born in the wet season (Hopley, pers comm.) (see Figure 10.1 Table 10.5).

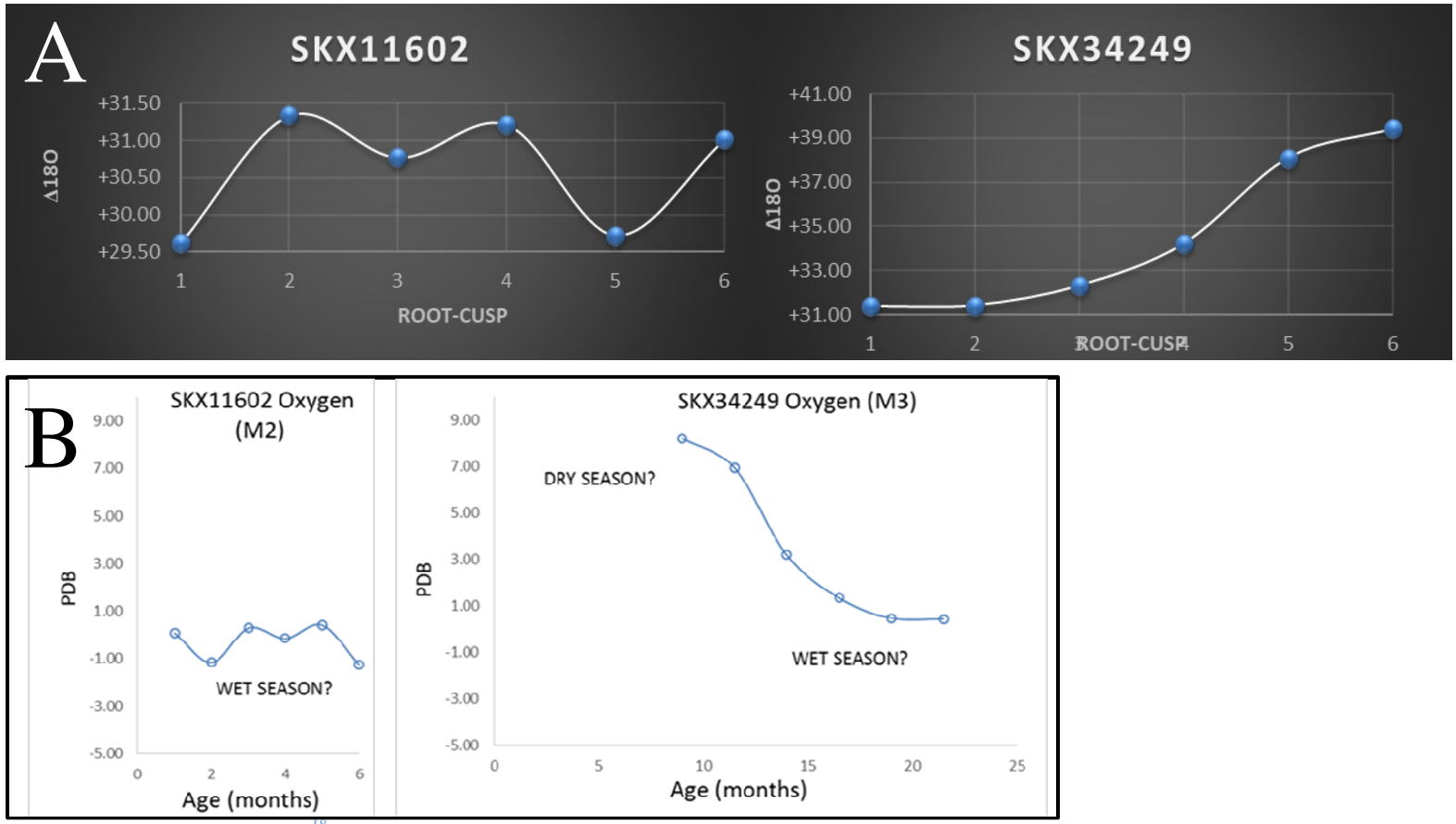


Figure 10.1: Oxygen isotope $\delta^{18}O$ values from serial sampled Antidorcas dental enamel. SKX 11602 is Antidorcas sp. from Swartkrans Member 1 LB. SKX 34249 is Antidorcas sp. from Swartkrans Member 3. The upper graphs (A) shows oxygen isotope values (SMOW) according to sample position from 1 (nearest root) to 6 (nearest cusp), the lower graphs (B) shows oxygen isotope values (PDB) according to relative age of the Antidorcas individual (Hopley pers.comm.).

Published sources isotope data

Published isotope data is combined with isotope data obtained during this research (above) to increase sample sizes and give a more complete picture, as can be gained from isotope analysis, for South African vegetation during this temporal period and comparative modern samples. These sources are used again when considering what the results from all methods combined can show us. This data is provided in Appendices A8, where specific references for each value used here are detailed. Published sources used here are: Luyt 2001; van der Merwe et al. 2003; Lee-Thorp et al., 1989, 1994, 2000, 2007; Sewell et al. 2019; Hare & Sealy 2013 (Hoedjiespunt c. 350-200 Ka, included for comparison of *Antidorcas* within southern Africa, whilst geographically and temporally separated from the Cradle of Humankind sites); Ecker et al. 2018; Sponheimer et al. 2003; Vogel 1978; Luyt & Sealy 2018; van der Merwe et al. 2013; Bocherens et al. 1996 (Djibouti c. 1.6 Ma, included for comparison of *Antidorcas* from a similar temporal period but geographically removed from the southern African *Antidorcas*).

The majority of published isotope data from South Africa used for comparative purposes here, quotes the oxygen isotope PDB scale. This study's data was calibrated using the SMOW scale and must be converted to allow comparisons between datasets. The scales are converted using the following formulae (Allen 1993):

$$\delta^{18}O\ PDB = (0.97006 \times \delta^{18}\ SMOW) - 29.94$$
$$\delta^{18}O\ SMOW = (\delta^{18}O\ PDB \times 1.03086) + 30.86$$

Table 10.4: Descriptive statistics for carbon ($\delta^{13}C‰$) and oxygen ($\delta^{18}O‰$) isotope values, mean, standard deviation (SD) and standard error (SEM) for each provenance, split by Antidorcas species.

Provenance	Species	$\delta^{13}C$ (PDB)‰				$\delta^{18}O$ (SMOW)‰			
		N	Mean	SD	SEM	N	Mean	SD	SEM
Sterkfontein Member 4	*A.recki*	9	-11.93	3.12	1.04	5	26.55	2.77	1.24
	A.bondi	2	-1.28	0.03	0.02	1	1.17	x	x
Swartkrans Member 1	*A.marsupialis*	9	-8.24	1.77	0.59	9	31.71	4.88	1.63
Sterkfontein Member 5	*Antidorcas sp.*	3	-6.02	5.85	3.38	3	31.03	3.59	2.07
	A.recki	5	-10.86	2.17	0.97	3	28.52	1.97	1.14
Swartkrans	*A.bondi*	9	-3.27	1.00	0.33	0	x	x	x
Swartkrans Member 2	*Antidorcas sp.*	5	-4.06	4.95	2.21	5	30.74	0.70	0.31
	A.recki	1	-12.90	x	x	0	x	x	x
	A.bondi	9	-1.09	2.77	0.92	9	30.74	1.42	0.47
	A.marsupialis	11	-7.82	5.92	1.79	11	30.54	1.40	0.42
Swartkrans Member 3	*Antidorcas sp.*	7	-8.28	1.17	0.44	7	34.01	3.41	1.29
	A.marsupialis	7	-7.27	2.09	0.79	7	33.91	2.99	1.13
Wonderwerk	*A.bondi*	1	-2.50	x	x	1	31.40	x	x
	A.marsupialis	6	-7.70	1.84	0.75	6	32.55	1.42	0.58
Djibouti, E.Africa	*A.recki*	1	3.00	x	x	1	28.60	x	x
Hoedjiespunt	*A.marsupialis*	5	-9.64	1.14	0.51	5	31.11	2.06	0.92
Modern	*A.marsupialis*	9	-12.42	2.41	0.80	7	35.41	0.80	0.30

Table 10.5: Descriptive statistics for carbon ($\delta^{13}C$‰) and oxygen ($\delta^{18}O$‰) isotope values, mean, standard deviation (SD) and standard error (SEM) for each fossil Antidorcas species.

Species	$\delta^{13}C$ (PDB)‰				$\delta^{18}O$ (SMOW)‰			
	N	Mean	SD	SEM	N	Mean	SD	SEM
Antidorcas sp.	15	-6.42	4.03	1.04	15	32.32	3.10	0.80
A.recki	9	-9.30	5.58	1.86	9	27.44	2.43	0.81
A.bondi	11	-1.23	2.52	0.76	11	30.84	1.29	0.39
A.marsupialis	45	-8.65	3.50	0.52	45	32.39	3.11	0.46

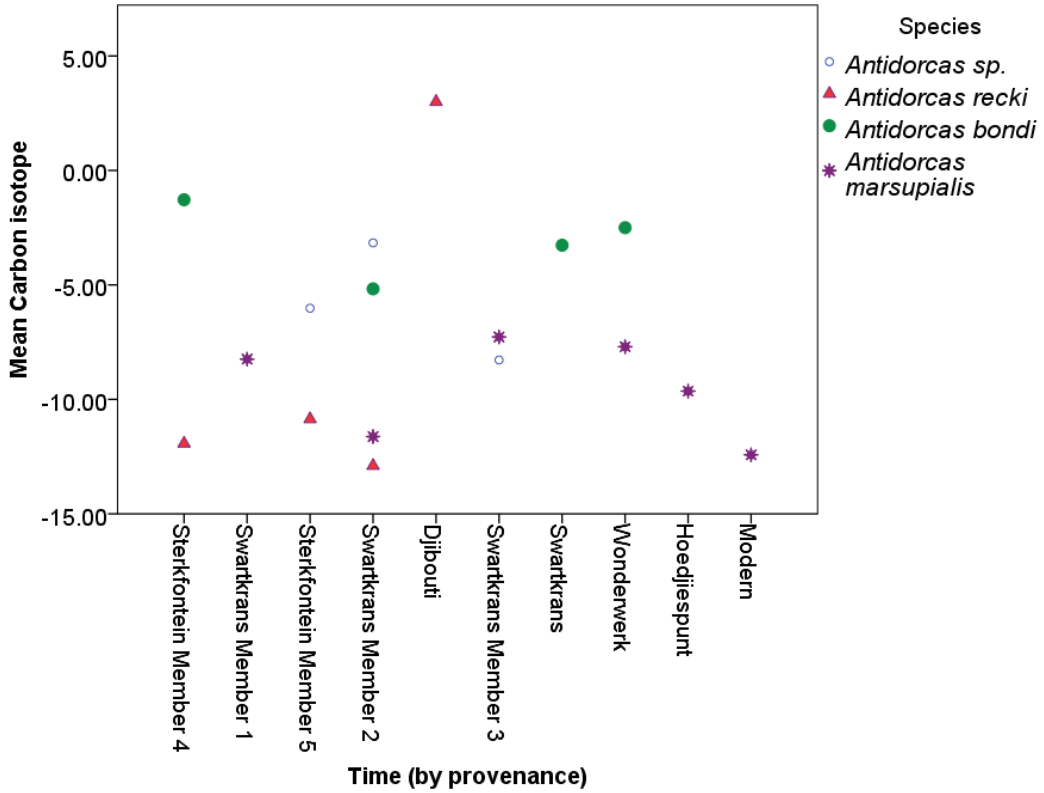


Figure 10.2: Scatterplot of mean carbon isotope values ($\delta^{13}C$ ‰) for each Antidorcas species through time (separated according to relative date of Member) before taxonomic re-assessment of Antidorcas dentition.

An increase in browsing is apparent for Swartkrans Member 2 prior to taxonomic re-assessment (Figure 10.2). However, when species are split, this apparent dietary divergence is not present, showing it to be an artefact of species averaging. This highlights the importance of taxonomic identification of species prior to analysis (Figure 10.3).

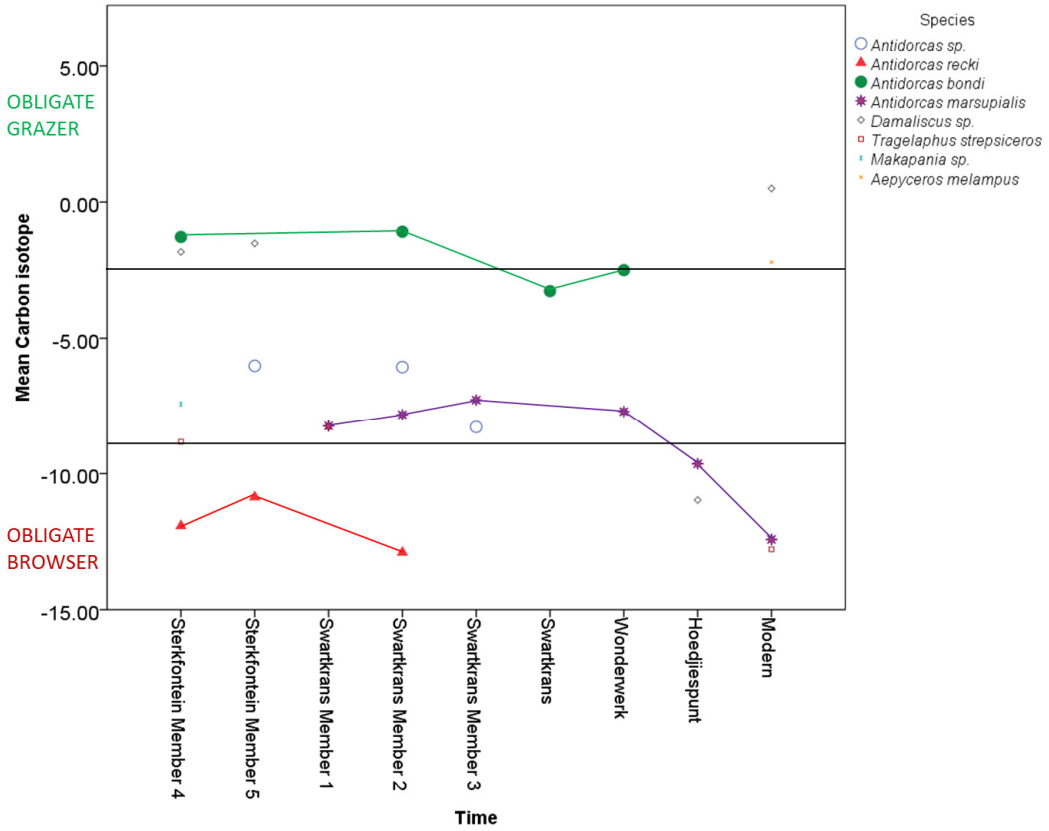


Figure 10.3: Scatter plot of mean carbon isotopes values ($\delta^{13}C$ ‰) through time for each species post-taxonomic identification reassessment of Antidorcas dentition (to highlight the value of taxonomic identification to as fine a level as possible) with supplementary species (along the grazing-browsing dietary spectrum) included for comparison to Antidorcas.

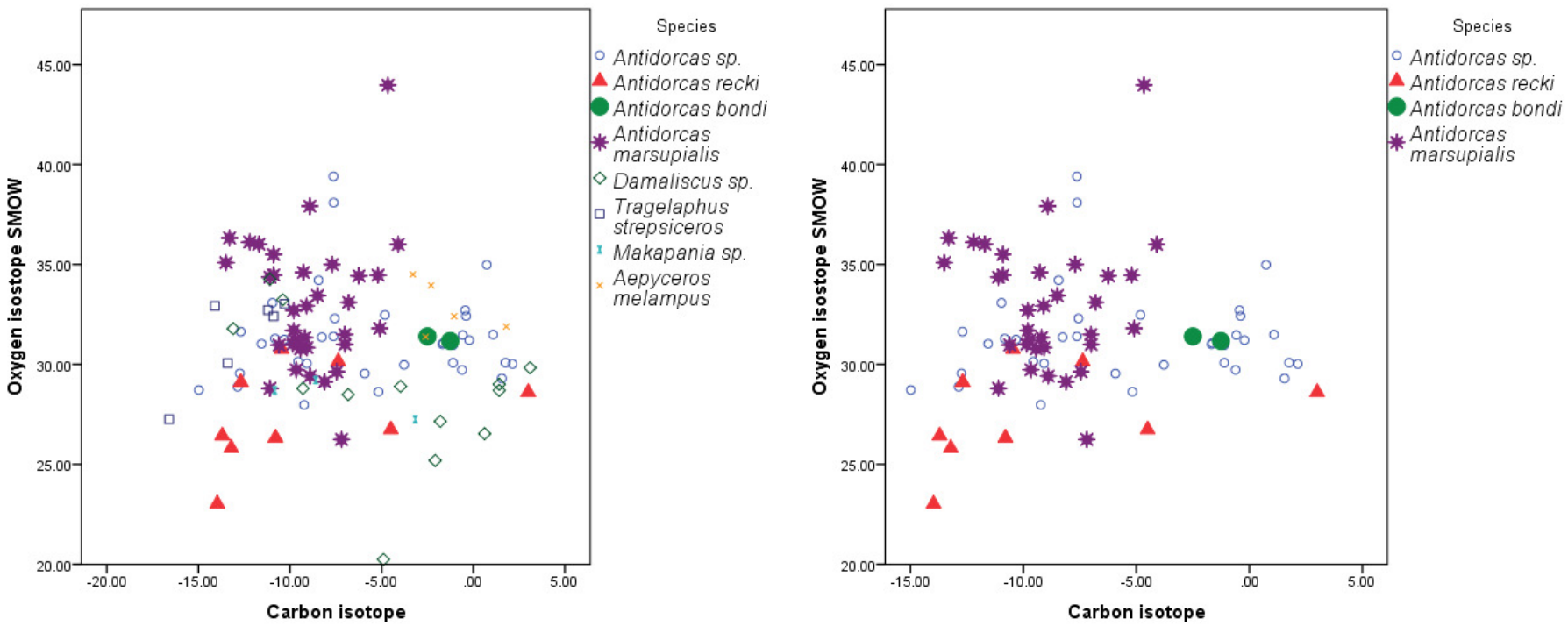


Figure 10.4: Left image: Scatterplot of stable isotope values, carbon ($\delta^{13}C$ ‰) against oxygen ($\delta^{18}O$ ‰), for Antidorcas and the supplementary species, used here to establish dietary parameters. Only individuals with both carbon and oxygen isotope values are displayed here. Right image: Scatterplot of Antidorcas only isotope values (to show more clearly without supplementary species being included). Only specimens with both carbon ($\delta^{13}C$ ‰) and oxygen isotope ($\delta^{18}O$ ‰) values are represented.

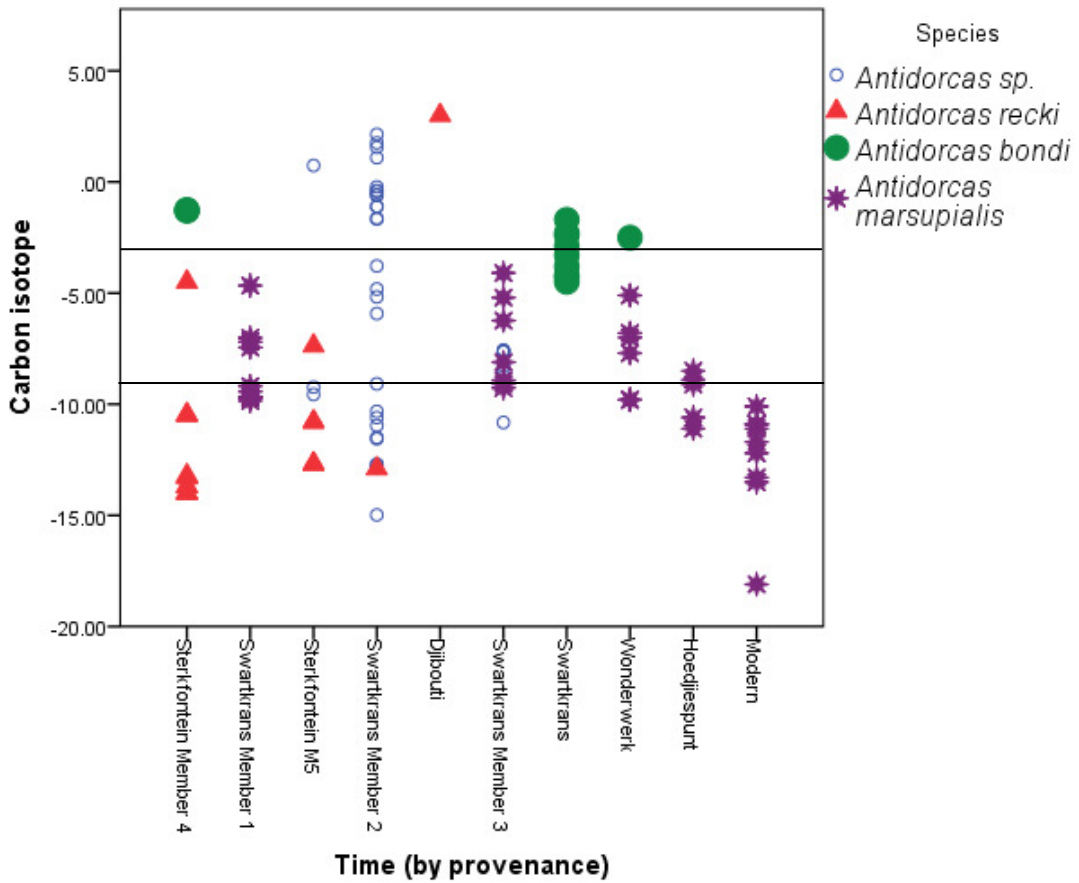


Figure 10.5: Published carbon isotope values (δ13C ‰) for individual Antidorcas specimens. Upper third delimits predominantly browsing diets, lower third, predominantly browsing diets, mixed-feeding diets in the centre. Dietary category values taken from Hare & Sealy (2013). Individual variation is apparent from this figure.

From this visual representation (Figure 10.5), Sterkfontein Member 4 and Swartkrans Member 2 appear to show population/character displacement and niche separation. Sterkfontein Member 4 shows a predominantly browsing group of *A. recki* and a mixed-grazing group, including *A. bondi*. Swartkrans Member 2 shows three groups, a browsing group, a mixed-feeding group and a grazing group, which Figure 10.3 highlights is likely character displacement by *Antidorcas* species.

Antidorcas marsupialis appear to gradually adopt a more consistently (intra-specific) browsing diet, from a more varied, mixed-feeding diet for individuals. Although some mixed-feeding is observed, *Antidorcas bondi* is typically grazing throughout. *Antidorcas recki* is consistently browsing in South Africa. The Dijbouti comparison comes from ca. 1.6 Ma *A. recki* (

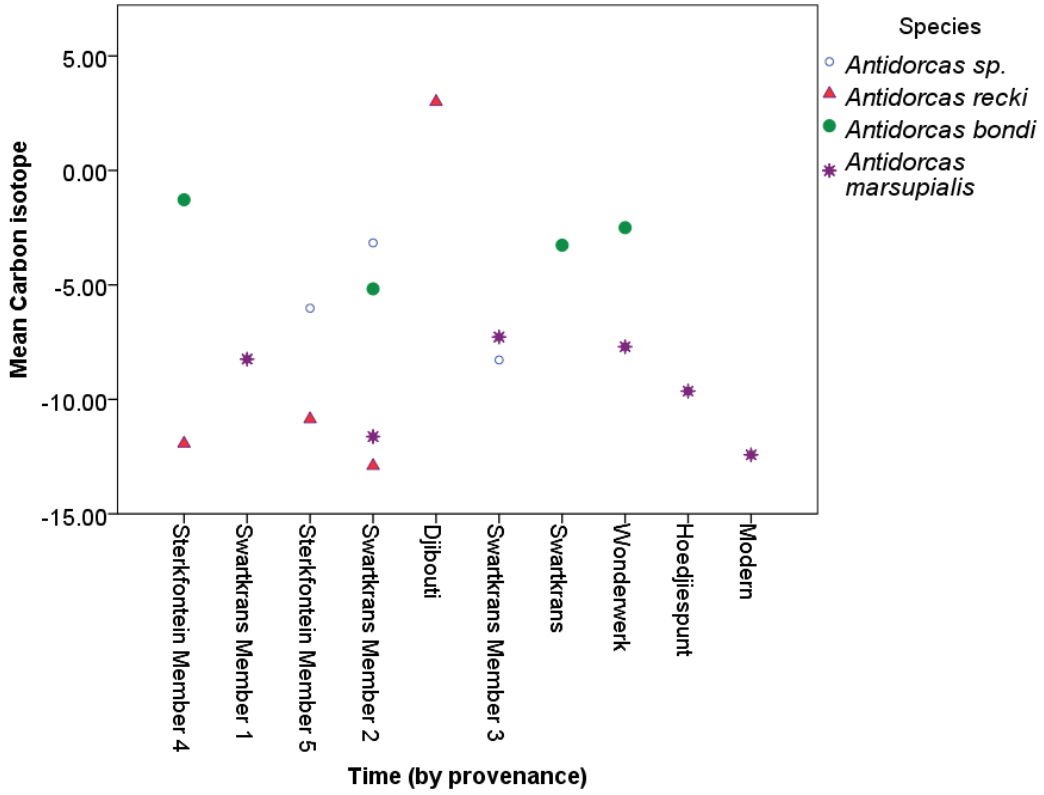


Figure 10.2 and Figure 10.3) and shows either that *A. recki* had the ability to consume predominantly grasses or that the East African *A. recki* is taxonomically different from those identified as *A. recki* in South Africa.

Table 10.6: Mean stable carbon and oxygen values and ranges for each Antidorcas species, for each Member (in chronological order).

Provenance	**Species**	**N**	**Mean δ13C (‰)**	**Range (‰)**	**Mean δ18O (‰SMOW)**	**Range (‰)**
Sterkfontein Member 4	*Antidorcas recki*	5	**-11.17**	1.78	**26.55**	7.73
	Antidorcas bondi	1	**-1.3**	x	**31.17**	x
Sterkfontein Member 5	*Antidorcas recki*	3	**-10.28**	5.31	**28.52**	3.81
	Antidorcas sp.	3	**-6.02**	10.3	**31.03**	7.01

Provenance	**Species**	**N**	**Mean δ13C (‰)**	**Range (‰)**	**Mean δ18O (‰SMOW)**	**Range (‰)**
Swartkrans Member 1	*Antidorcas marsupialis*	9	**-8.24**	5.19	**31.71**	17.73
Swartkrans Member 2	*Antidorcas* sp.	5	**-4.06**	11.59	**30.74**	1.66
	Antidorcas bondi	9	**-1.09**	7.69	**30.74**	4.08
	Antidorcas marsupialis	11	**-7.82**	17.12	**30.54**	4.36
Swartkrans Member 3	*Antidorcas* sp.	7	**-8.28**	3.26	**34.01**	8.11
	Antidorcas marsupialis	7	**-7.27**	5.17	**33.91**	8.78
Wonderwerk	*Antidorcas bondi*	1	**-2.50**	x	**31.40**	x
	Antidorcas marsupialis	6	**-7.70**	4.70	**32.55**	4.00
Hoedjiespunt	*Antidorcas marsupialis*	5	**-9.64**	2.60	**31.11**	4.64
Djibouti	*Antidorcas recki*	1	**3.00**	x	**28.60**	x
Modern	*Antidorcas marsupialis*	7	**-11.94**	2.60	**35.41**	1.96

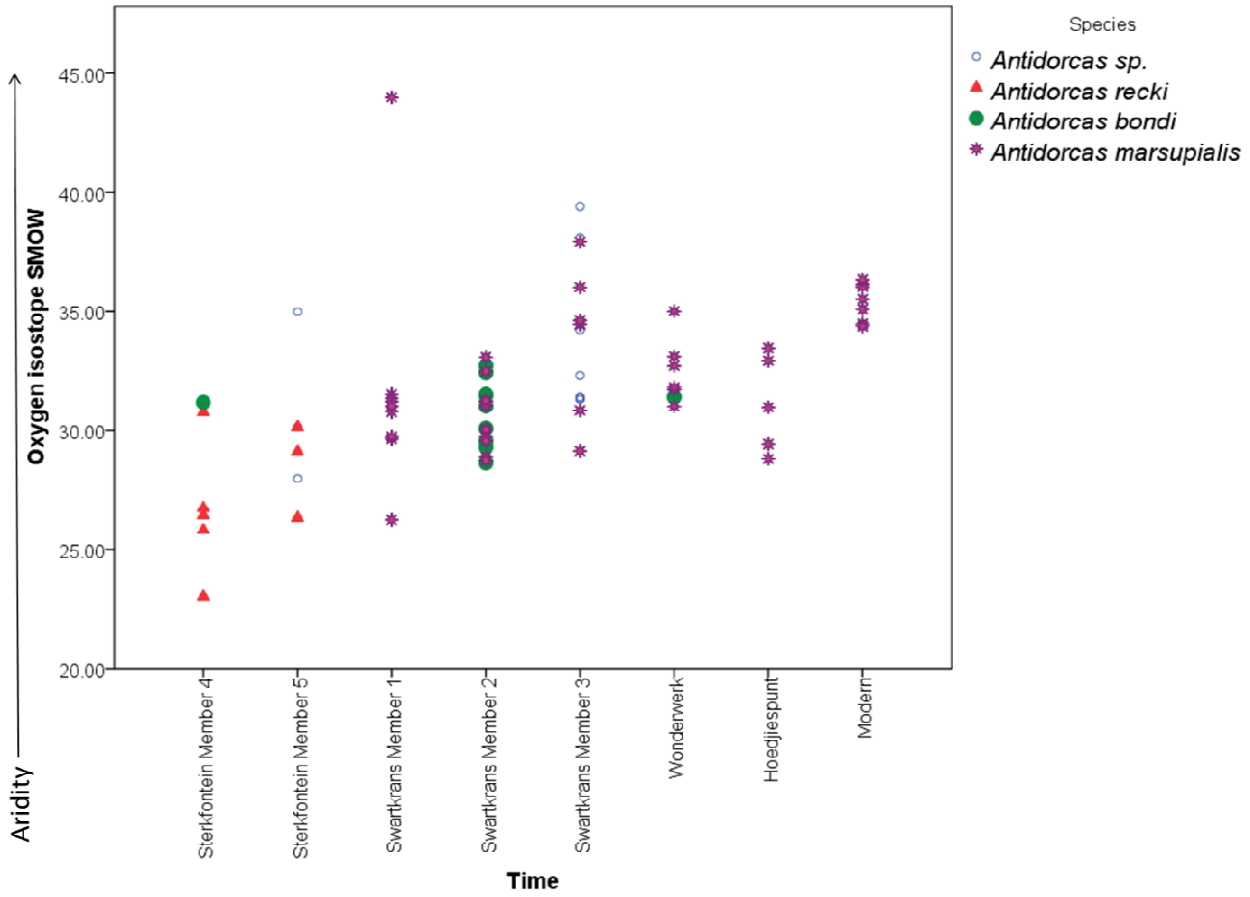


Figure 10.6: Antidorcas oxygen isotope values ($\delta^{18}O$ ‰) through time (according to provenance), separated by species.

When looking at the individual values, *Antidorcas* is consistently showing mixed feeding patterns through time. This may represent the differing species dietary and habitat preferences. This is certainly the case for the difference observed in Sterkfontein Member 4. The individuals with more depleted carbon isotopes are *A. recki* and those with higher carbon isotope values represent *A. bondi.* Alternatively, perhaps differentiated (as observed in the modern springbok by e.g. Bigalke 1972; David 1978), that male and female herds, which live separately for the majority of the year, will occupy different habitats. That being said, dental enamel isotope values represent the time period in the individual's life of enamel formation and mineralization, i.e. when they are young. The values may still represent young males and females differentially finding their adult place in the landscape. Or perhaps, rather than a sexual dimorphism in diet, represent slightly differing lifetime gaps, indicting a dietary shift ontogenetically. The only real mixed-feeding signal for the genus, rather than for individuals, is seen in Swartkrans Member 3, where *A. marsupialis* dominates. A similar trend is seen for oxygen isotopes (Figure 10.56). However, there is the potential that these trends are affected by sampling bias, with larger sample sizes for the younger time periods.

10.2.1 Statistical Analysis

Only *Antidorcas marsupialis,* as a species, showed variation through time for either carbon or oxygen isotopes. *Antidorcas recki* and *Antidorcas bondi,* as species did not significantly alter isotope values through time. An independent samples Kruskal-Wallis test showed *A. marsupialis* to have significantly different carbon (p=.001) and oxygen (p=.009) values through time (according to member). *Antidorcas* sp. also showed variations in oxygen (p=.002) isotopes through time but this likely due to mixing *Antidorcas* species.

Those identified as *'Antidorcas* sp' from Swartkrans Member 2 (Sewell et al. 2019) were re-examined to establish species identification. This was done by cross-referencing to the dataset created here and looking at the photographs taken of the individual teeth. The majority were *Antidorcas bondi*, yet this had no bearing on significant differences through time. This suggests that *Antidorcas* species' diet in Swartkrans Member 2, as reflected by stable isotope values were not significantly different to other deposits for *A. bondi* or *A. recki*.

Carbon

Kruskal-Wallis independent samples test show significant differences for through time for $\delta^{13}C$ for *Antidorcas marsupialis* (p<.000).

The same test showed significant differences between species only for Sterkfontein Member 4 (p=.036).

Mann Whitney-U pairwise comparisons with Bonferroni adjusted significance levels for *A. marsupialis* through time showed Swartkrans Member 1 (mean= -8.24‰) had significantly higher (less depleted in carbon) $\delta^{13}C$ values (p<.000) than modern *A. marsupialis* (mean= -12.42‰). Swartkrans Member 3 had significantly less depleted $\delta^{13}C$ values than modern specimens (p<.000) and Wonderwerk (mean = -7.70‰) had significantly higher $\delta^{13}C$ values than Modern (p<.000).

In Sterkfontein Member 4, *A. recki* (mean=-1.93‰) had significantly more depleted $\delta^{13}C$ than *A. bondi* (mean= -1.28‰) when comparing only *Antidorcas* species (p=.036). *A. recki* had significantly more depleted $\delta^{13}C$ values than *Damaliscus* sp. (mean= -0.22‰) when all species were included (p<.000).

Oxygen

Kruskal-Wallis independent samples test show significant differences through time for $\delta^{18}O$ for both *Antidorcas* sp. (p=0.042) and for *Antidorcas marsupialis* (p=0.004).

No significant differences were found across species for any provenance.

Mann Whitney-U pairwise comparisons with Bonferroni adjusted significance levels for *A. marsupialis*, this significant difference was found (p<.000) to be significantly lower for Swartkrans Member 2 (mean= 30.54‰) than for modern specimens (mean = 35.41‰).

For *Antidorcas* sp., significantly lower $\delta^{18}O$ values (p=.009) for Swartkrans Member 2 (mean= 30.74‰) were found compared to Swartkrans Member 3 (mean= 34.01‰). However, as '*Antidorcas* sp.' represents individuals only identified to genus level, these samples may represent differential *Antidorcas* species compositions.

10.3.2 Individual variation

'Outliers' exist within the dataset that highlight the degree of individual variability evident from stable isotope analysis. For instance, SKX 10703, *A. marsupialis* from Swartkrans Member 1 displays the highest carbon $\delta^{13}C$ value (-4.66‰) and highest oxygen $\delta^{18}O$ (43.97 ‰ SMOW), where other *A. marsupialis* from Swartkrans Member 1 have values in the range of -9.85 to -7.01‰ and +26.24 to 31.50‰, for carbon and oxygen respectively.

Sterkfontein Member 5, (considered roughly contemporary with Swartkrans Member 1) individual highest carbon $\delta^{13}C$ value is S94-7314, at +0.74‰, with the other individuals ranging from -7.37 to -12.68‰. The same individual yields the highest oxygen $\delta^{18}O$ content, at 34.98‰, where the other individuals in the assemblage range between 26.32 and 30.14‰ SMOW. The isotope values from this assemblage come from *A. recki* or *Antidorcas* sp.

Sterkfontein Member 4, all *Antidorcas* (here, *Antidorcas recki*) range within the obligate browsing, with depleted carbon isotope values below -10‰ $\delta^{13}C$, other than one individual-STS 1596, which displays mixed-feeding values (-4.50‰ $\delta^{13}C$).

Swartkrans Member 2 displays 4 dietary groupings from individual variation, indicative perhaps of greater habitat heterogeneity. Swartkrans Member 2 displays 4 dietary groupings from individual variation (Figure 10.7). This cannot be explained by species dietary differentiation. Habitat heterogeneity is suggested. *Antidorcas* sp. and *A. marsupialis* are predominantly browsing, with some mixed-feeding, or within the range of obligate grazing. *A. bondi* ranges from obligate grazing, as would be expected for the species, to mixed-feeding. Individual variation appears to only be noteworthy for Swartkrans Member 2.

Swartkrans Member 3 *Antidorcas*, predominantly *A. marsupialis* fall within the mixed-feeding to browsing $\delta^{13}C$ range.

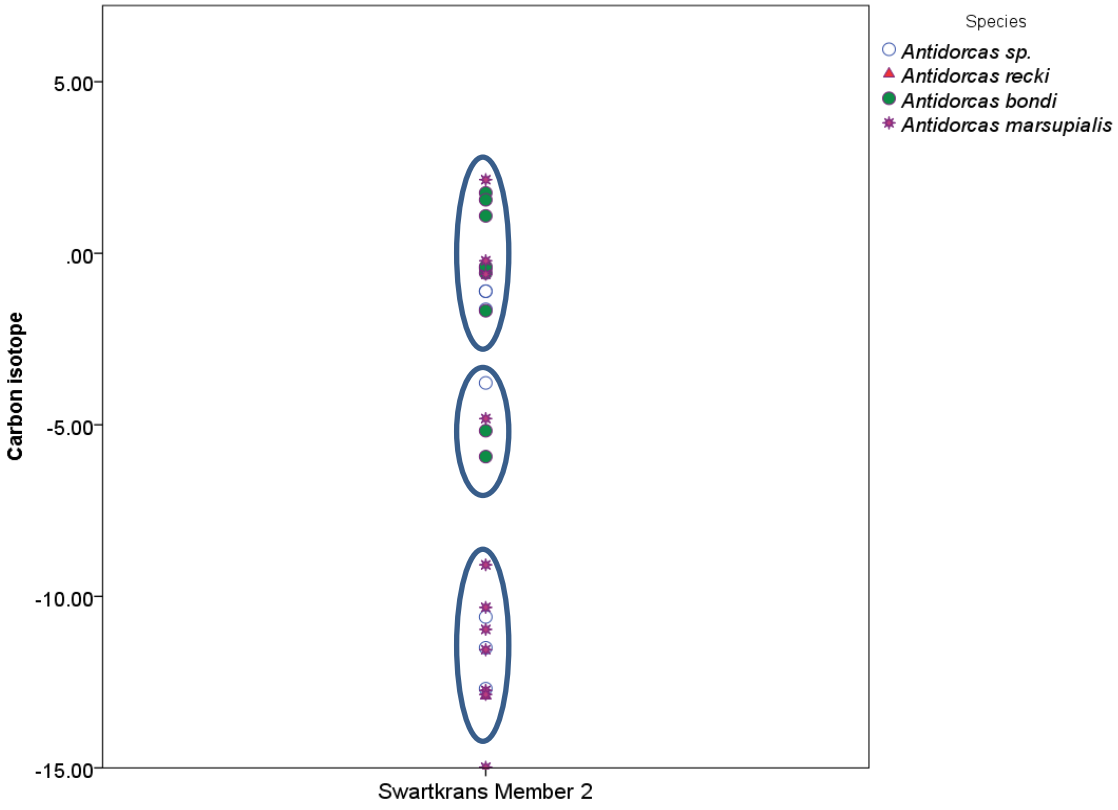


Figure 10.7: Individual variation in stable carbon isotope values (δ13C ‰) for Swartkrans Member 2. Dietary groupings are shown in blue (from top to bottom: grazing, mixed-feeding, browsing).

10.3 DISCUSSION

Results are discussed at a local scale initially, before being placed into a wider southern African context. It has been argued for both modern (e.g. Kohn et al. 1996; Luyt 2017) and South African fossil (e.g. Sponheimer & Lee-Thorp 1999a) bovids that browsers are more enriched in $\delta^{18}O$ compared to grazing taxa. This is a result of evaporatively enriched ($\delta^{18}O$) leaves being consumed by browsers in arid environments. However, the opposite is found here, supporting that found in East African bovids (Bocherens et al. 1996), which was postulated to be due to arid conditions requiring the closure of C_3 plant stomata, reducing evapotranspiration water loss. The complexities of the modern savanna ecosystem and the seasonal variability, particularly in rainfall, impacting upon the water retention in C_3 (with deep roots) and C_4 plants (with shallow roots) differentially has been argued to play a part. With increased seasonality, C_3 plants have the capability to continue constant evapotranspiration levels, where C_4 plants do not. That opposing results have been found here for *Antidorcas* may invoke either a discussion on the role of CAM plants, such as succulents, within the ecosystem as a known constituent of modern *Antidorcas* diet. Consuming CAM plants is likely to provide enriched $\delta^{13}C$ values, in a similar way to C_4 grass inclusion. Alternatively, these patterns are opposing because of the water-independence of *Antidorcas*. Again though, consuming leaves that are enriched in $\delta^{18}O$ compared to grasses, would suggest browsing *Antidorcas* should display enriched $\delta^{18}O$ values.

Sponheimer & Lee-Thorp (1999a) suggest the slight enrichment in *A. bondi* $\delta^{18}O$ compared to obligate grazers (such as *Equus*) was due to feeding on fresh, new grass shoots (Sponheimer and Lee-Thorp 1999a; Brink & Lee-Thorp 1992) and was therefore, less dependent on standing water. Coupled with the use-wear evidence, it is suggested that although feeding on new shoots may play a part, *A. bondi*'s slight enrichment is likely due also to an inclusion of C_3 vegetation to a greater extent than more habitual grazers. This feeding difference is also likely to impact on water consumption, again altering the $\delta^{18}O$ value obtained.

Adaptations to heat stress also impact upon $\delta^{18}O$ levels. For example, nocturnal herbivores consume plants when they are less enriched in $\delta^{18}O$ (which peaks during the midday heat), and by not exposing themselves to the midday heat, they do not have to reduce their body temperature by sweating or panting (Sponheimer & Lee-Thorp 1999a). Modern *Antidorcas* typically feed during the cooler periods of the day, seeking shade where necessary. Consequently, isotope values would be expected to be reflective of consuming perhaps C_3 vegetation, which is typically in greater abundance in shady areas and of increased plant moisture compared to herbivores feeding continually throughout the day. This would likely manifest as depleted $\delta^{13}C$ values and enriched $\delta^{18}O$ values. Values for Swartkrans Member 1 and Member 3 *Antidorcas* often (but not exclusively) follow this pattern. Swartkrans Member 3 serial sampled individuals hint at seasonality, alternating between carbon and oxygen acting in opposition (i.e. when $\delta^{13}C$ is depleted, $\delta^{18}O$ is enriched) and acting together (both $\delta^{13}C$ and $\delta^{18}O$ enriched/depleted together). When this is not the case for fossil *Antidorcas*, different palaeoenvironmental conditions to those seen today must be inferred, possibly along with differing behavioural reactions of fossil *Antidorcas*.

It is suggested that the depleted $\delta^{18}O$ witnessed for the browsing *Antidorcas* in this dataset are due to environmental conditions. Wetter palaeoenvironmental conditions allow *Antidorcas* to be more reliant on drinking water (opportunistically when there is more water availability), resulting in less enrichment of $\delta^{18}O$. Variations within each member may reflect seasonality, particularly in the members representative of the later time periods, or reflect individual animal dietary fluctuations. Where the $\delta^{18}O$ values do not appear to correlate to the $\delta^{13}C$ values, palaeoenvironmental factors are suggested to be playing a greater role than diet.

Decoupling palaeoenvironmental signals from dietary signals can be complex (as seen by a lack of consistently correlating $\delta^{13}C$ and $\delta^{18}O$ values). Using the mixed-feeding *Antidorcas marsupialis*, fluctuations in palaeoenvironmental conditions can be more reliably inferred, (rather than a reflection of dietary ecology). In a mixed-feeder, $\delta^{13}C$ values are indicative of palaeovegetation availability (C_3/C_4) and $\delta^{18}O$ values reflective of palaeohydrological factors (depleted $\delta^{18}O$ indicative of reduced evapotranspiration and therefore, of wetter palaeoenvironments).

Mean values for modern *A. marsupialis* indicate browse-dominance ($\delta^{13}C$ -12.42‰) in arid environments ($\delta^{18}O$ 35.41‰). Fossil *A. marsupialis* indicates mixed-feeding in Swartkrans (Members 1-3) ($\delta^{13}C$ -8.24‰ SKX M1, -7.82‰ SKX M2, -7.27‰ SKX M3) with gradually increased inclusion of C_4 vegetation apparent. This trend of slight $\delta^{13}C$

enrichment indicates, via fossil *A. marsupialis,* a very marginal increase in grasslands. Alongside *A. marsupialis* oxygen values, a marginal increase in aridity from Swartkrans Member 1 ($\delta^{18}O$,31.71‰) to Swartkrans Member 3 ($\delta^{18}O$ 33.91‰) with a temporary slightly less arid period during Swartkrans Member 2 ($\delta^{18}O$ 30.54‰) is inferred.

Seasonality

A correlation, showing increased browse consumption (depleted $\delta^{13}C$ values) with depleted $\delta^{18}O$ values, may suggest wetter conditions. Whereas during the dry season, browse (leaves) would be expected to have enriched $\delta^{18}O$ values due to increased evapotranspiration. Where seasonality increases during the Pleistocene, this may be reflected in the *Antidorcas* isotope values. Further sampling would be required to identify this pattern conclusively.

Antidorcas palaeoecology

The two serial samples gained from this study, SKX 11602 and SKX 34249 are consistent with animals being born at the start of the wet (rainy) season. Modern *Antidorcas* will adjust their lambing season according to environmental conditions, timing the mating and lambing behaviour to coincide with times of greater resources abundance (Estes 1991; Skinner and Louw 1996). The possibility exists that this was not the case for all temporal periods represented by this fossil record. Periods of environmental instability would make lambing less predictable with the potential that lambs are born throughout the year. The season of birth can be shown via serial isotope sampling of dental enamel but would require much greater sample sizes to show this.

Review of method

Due to the destructive nature of isotope sampling, research is always subject to limited sample sizes. Here, permission was granted on already broken specimens and none of the specimens sampled for isotope analysis were viable for microwear analysis to allow a direct comparison.

One major positive of this technique is its lack of assumptions. Other than the assumption of the specimens' autochthonous character (i.e. indigenous); isotopes enable the use of bovids, which are abundant and dependent on the local and available vegetation, to provide an environmental signal that has not relied upon assumptions about the behaviour of fossil taxa (Luyt 2001). Caution should be taken to ensure that the species was not migratory, yet this would likely be shown up in a skewed population demographic. For example, a lack of females and juveniles may be indicative of a migrating bachelor herd. Yet in this instance, the research question is concerned about the palaeoenvironment on a regional scale (i.e. not site-specific), that would still be captured even by a migratory species

Perhaps bulk sampling has a tendency to favour grazing signals, with less depletion in $\delta^{13}C$ within enamel samples. SKX34249 was analysed with both serial and bulk sampling. The serial sample shows clear mixed feeding values, with the bulk sample showing mixed feeding but with a greater C_4 component (Table 10.3).

Local scale (Cradle of Humankind)

Oxygen isotopes can vary between regions, as animals alter their drinking habits according to the local environment.

$\delta^{13}C$ results show an increase in grazing through time for *Antidorcas*. As a species, greater grazing signals ($\delta^{13}C$ enrichment indicating more C_4 grass consumption) are obtained from *Antidorcas bondi,* supporting Brink and Lee-Thorp (1992). Contrastingly, more browsing ($\delta^{13}C$ depletion and C_3-vegetation dominance) is yielded for *Antidorcas recki,* supporting Lee-Thorp et al. (2007).

However, Swartkrans Member 2 (c.1.7 Ma) appears to show slightly less aridity ($\delta^{18}O$) than surrounding Members, supporting the increased browsing signals suggested via DMTA, and perhaps the increased variability pattern evidenced by mesowear for Swartkrans Member 2.

'Micro'-habitats

Similar to Cuthbert et al (2017)'s finding in East Africa, that persistent groundwater acted as hydro-refugia to buffer climatic variability, 'micro' habitats ('micro' here is used to mean an area inhabitable by *Antidorcas*/medium-sized animals) could provide these refugia in southern Africa. On the smallest scale in which *Antidorcas* and hominins could be affected, areas closest to water sources are likely to retain trees and other moisture dependent vegetation through more arid conditions (compared to open landscapes further away from an immediate water body, such as a river), providing more shelter and keeping a 'micro' climate within the immediate vicinity of the water source. The shelter of the trees provides an area of shelter for thermoregulation, away from the direct sunlight exposure, as well as more protection from predators than open landscapes and vegetation with increased moisture content to eat; all of which would be appealing to *Antidorcas*. For these types of habitats to prevail, aridity would need to remain under a threshold aridity level (where the river is still viable), in order to maintain some degree of mosaic habitat landscape.

For example, Swartkrans is situated closer to the Blaubank river than Sterkfontein and in a modern context, can be seen to support more C_3 vegetation (trees and water-dependent floral taxa) in the immediate vicinity than the nearby (<2km) exposed Sterkfontein area (see chapter 2). However, no significant differences in the mean stable isotope values were apparent between Sterkfontein Member 5 and Swartkrans Member 1, which are considered to have been deposited during roughly contemporary temporal ranges (and might indicate the impact of local factors if significant differences were apparent).

Palaeoecology of *Antidorcas:* Carbon and Oxygen Isotopes

Antidorcas bondi $\delta^{13}C$ values reflect typical grazing signals and *Antidorcas recki* reflects typical browsing signals. *Antidorcas marsupialis* appears to show a gradual trend towards increased C_3 composition in diet, perhaps at odds with the spread of grasslands and aridity. This implies that mixed habitats and resources were available throughout, and the sample *Antidorcas* represent either a mix of seasonal signals, or reflect the individuals' preference that happen to be in the assemblage. Alternatively, the increase in *A. marsupialis* C_3 consumption could be indicating an increase in competition from more specialised grazers as grasslands increase, forcing the springbok to increase browsing. The oxygen isotope

signals are more varied and it is likely that within these values, the catalyst of the shift in diet can be extrapolated.

When attempting to reflect any changes in vegetation, using a mixed feeding antelope appears to be of greater benefit than using species with more specialist diets. The more specialised species tend to reflect only their palaeoecology, whereas the mixed feeder is more faithfully reflective of the fluctuating palaeovegetation.

Palaeoenvironment of South Africa through time: Carbon isotopes

Using published isotope records, *Antidorcas marsupialis* originally showed mixed-feeding preferences through carbon isotope values for Swartkrans Member 1 and 3, but Swartkrans Member 2 showed values more similar to the modern signals of predominantly browsing dietary signals.

Swartkrans Member 2 appears to differ from surrounding temporal periods, with the decreased oxygen content suggesting increased precipitation compared to the earlier Member 1 and later Member 3. Although the carbon isotope values are not statistically significant, the depleted carbon $\delta^{13}C$ values for Swartkrans Member 2 support this suggestion. That *Antidorcas bondi* maintains a predominantly grazing signal, albeit with depleted carbon $\delta^{13}C$ values for this temporal range (c.1.7-1.07 Ma), along with elevated individual variation, suggests an element of habitat heterogeneity was supported (likely a higher degree of habitat heterogeneity across the landscape).

After inputting my taxonomic identifications to specimens whose isotope values were gained from published data, more individuals were assigned to species level. Following this, analysis showed that Swartkrans Member 2 *A. marsupialis* had only slightly depleted carbon isotope values compared to Swartkrans Member 3 *A. marsupialis* and slightly more enriched for Swartkrans Member 2 *A. marsupialis*, than in Swartkrans Member 1. This indicates a steady increase in C_4 plants from Swartkrans Member 1 through to Member 3 but with a consistently mixed feeding signal throughout. Oxygen isotope values however, maintain significant depletion in Swartkrans Member 2, in spite of the tighter species classification. This therefore still suggests increased precipitation c.1.7-107 Ma (Swartkrans Member 2).

More significant differences were found before species identification was tightened. The prevailing discussion rests on the correct taxonomic classification of specimens, lending justification to the need for palaeoecological investigation into fossil species prior to further investigative analysis to reconstruct palaeohabitats.

As found by Maxwell et al. (2018), sampling and taphonomic bias can produce false indications. A ‘pulse’ of environmental instability was suspected for Swartkrans Member 2 prior to reconsideration of taxonomic classification, where Swartkrans Member 2 *A. bondi*, the faithful grazer (Brink & Lee-Thorp 1992; Brink 2016) showed mixed feeding signals. Although *A. bondi* shows some signs of not necessarily being as faithful a grazer as was originally hypothesized (Brink & Lee-Thorp 1992), this may have been somewhat exaggerated. Adopting a more generalist dietary behaviour during times of environmental instability would make evolutionary sense, as could have been inferred from the misleading

isotope mean signal gained from *A. bondi* in Swartkrans Member 2 prior to further analysis (Figure 10.2, Figure 10.3, Figure 10.7). This distinction shows that considering the individual diets as well as the mean values is of importance, as well as then considering factors such as seasonality and sexual dimorphism to explain any apparent shift in dietary behaviour, especially from small sample sizes. Environmental instability and temporally increased habitat heterogeneity for c.1.7-1.078 Ma (Swartkrans Member 2) is suggested (Figure 10.7).

However, when considering the *Antidorcas* individual specializations (Lehmann et al. 2015), Sterkfontein Member 4 and Swartkrans Member 2 show the most variability in carbon isotope values, with 2 or 3 groups respectively, forming, reflecting the grazing-browsing dietary preferences and population displacement, which is likely to reflect the dietary preference of each *Antidorcas* species rather than intra-specific differential dietary specialization.

During times of resource scarcity, increased partitioning of food resources to form isotopically distinct dietary niches for each of the *Antidorcas* species can increase the likelihood of survival. As was found (Lehmann et al. 2015) for the modern springbok, co-existing alongside the gemsbok (*Oryx gazella*) in a desert ecosystem.

Palaeoenvironment of South Africa through time: Oxygen isotopes

Depleted $\delta^{18}O$ evidenced in Swartkrans Member 2 suggests increased precipitation levels during deposition of this Member.

An initiation of the seasonality experienced today with the onset of the Walker circulation ca. 1.7 Ma, would explain why we see dietary changes and more discord between methods (representative of differing ontogeny stages of an individual), according to seasonal availability of resources.

Physiological adaptations to heat stress differentially impact the levels of $\delta^{18}O$ lost via the nose, mouth or skin (water vapour is depleted in $\delta^{18}O$) during thermoregulation (Wong et al. 1998; Lee-Thorp and Sponheimer 2000; Sponheimer and Lee-Thorp 2001; Luyt 2001). In this way, Oxygen isotope values can be indicative of fossil species thermoregulatory mechanisms when compared with other species. When looking at many species with the same response, the $\delta^{18}O$ values can indicate aridity levels (via group response to heat stress, or a lack thereof). *Antidorcas*, as a combined genus, indicates a gradual enhancement in $\delta^{18}O$ through time, suggesting a trend of gradually increasing aridity through time (Figure 10.6).

With an increased sample size, the advised screening process (Faith 2018) to ensure fossil taxa follow their modern counterparts in being evaporation sensitive/insensitive would be worthwhile. The screening process requires the consideration of carbon $\delta^{13}C$ levels to infer grass consumption and the application of use-wear analysis to interpret the relative C_3/C_4 grass composition of such diets. Following this process, aridity levels can be accurately deduced (Faith 2018).

10.4 SUMMARY

- *Antidorcas bondi* $\delta^{13}C$ values reflect typical grazing signals and *Antidorcas recki* reflects typical browsing signals.
- *Antidorcas marsupialis* indicates a marginal increase in aridity and grasslands from Swartkrans Member 1 (2.0-1.4 Ma) to Member 3 (1.5-0.61 Ma), with a temporarily less arid phase during Swartkrans Member 2 (1.7-1.07 Ma).
- Swartkrans Member 2 appears to markedly differ from surrounding temporal periods, with increased individual animal dietary variation evident for *Antidorcas,* and lower oxygen values, suggesting lower aridity than earlier, or later, temporal periods. A period of increased habitat heterogeneity and environmental instability c. 1.7-1.07 Ma (Swartkrans Member 2) is suggested.
- As a genus, *Antidorcas* stable isotope values (carbon and oxygen) reflect the gradual trend towards increased aridity, with open habitats and C_4 grasslands by a weak positive correlation of isotope values with time. Yet *A. marsupialis* are incorporating progressively more browse in the diet through time (potentially due to biotic competition but still reflective of browse presence in the landscape).

CHAPTER 11

Multi-Method Analyses

The novelty of this research lies in the use of multiple complementary methodologies, combined to provide a holistic palaeovegetational signal, via the bioproxy of the *Antidorcas* taxa, through time. In this chapter, the results obtained from each method are compared and combined statistical analyses and interpretations are presented. Initially, individual specimens that were subjected to multiple methods are analysed to understand the differential signals obtainable for an individual, via each method. Equipped with the knowledge of how the signal from each method may appear from one individual, the whole dataset is then considered. This chapter is intended as a summary chapter.

11.1 INTRODUCTION

Using multiple complementary methods has been shown to provide a more complete palaeoenvironmental reconstruction than would be viable from a single method approach (e.g. Rivals et al. 2015; González-Guarda et al. 2018; Sewell et al. 2019; Strani et al. 2018). Schubert et al.'s (2006) multi-method (stable carbon isotopes, microwear and mesowear) analysis of Makapansgat Limeworks (South Africa) bovids and Blondel et al.'s (2018) study on fossil Tragelaphines also highlight the importance of using a multi-method approach, in order to understand the palaeoecological data as an holistic picture. Thus, allowing for more accurately determined inferences and reconstructions from the differential information and perspective each method yields for fossil bovids.

Particularly if the bioproxy used is a mixed-feeder, capable of reflecting multiple smaller habitats available across the landscape (e.g. Jones and DeSantis 2017; Ecker et al. 2018; Sewell et al. 2019; Strani et al. 2018), multi-method approaches are beneficial. Yet presently, there remains relatively few multi-method analyses of diet in the literature, particularly so, those which concentrate on the palaeoecology and inferred palaeovegetation indicators from fossil antelope. One such study, by Louys et al. (2012), compares the significance of correlations between data obtained from isotope values, raw molar measurements and mesowear values. Their study, which highlights the validity of mesowear as a method for determining antelope diets, shows a positive correlation between stable carbon isotope values and mesowear variables (occlusal relief and cusp shape). The expected pattern of cusp sharpness and $\delta^{13}C$ was shown to be consistent with the rationale that an increase in C_4 grass consumption (evidenced via carbon isotopes) is correlated to a decrease in cusp shape (due to the abrasive nature of grass particles). Yet unexpectedly, low relief was found to increase as the consumption of C_4 decreased. This study also found that species-averaged mesowear variables did not correlate as well with stable carbon isotope values, as their individual specimen-by-specimen values did (Louys et al. 2012), lending support for the implementation of such a dual approach here.

Moreover, mesowear variables [high dental occlusal relief and rounded cusps] are believed to be positively correlated with mean annual precipitation, water balance and humidity (Kaiser and Schulz 2006), and palaeoenvironmental reconstructions could therefore benefit from being complemented by oxygen isotope analysis.

Each method reflects a slightly differing temporal scale from the *Antidorcas'* lifetime. A multi-method approach can be used to mitigate for the limitations inherent in each method. Although each method has its merits, they can only inform so far for each palaeodietary or palaeoenvironmental research question, each offering different degrees of temporal lag and operating at slightly conflicting geographical ranges (e.g. Meadows 2015; Stewart and Mitchell 2018). A combined methods approach can hope to buffer some of the issues with the assemblages used, such as time-averaging, by capturing differing lifetime scales from the combination of dietary proxies. For example, seasonality within the assemblage may be obscured by time-averaging of deposits. However, by applying many dietary methods to individual specimens, seasonal-feeding and seasonal palaeoenvironmental changes become more visible.

The complexity of site stratigraphy and the potential confounding factors of averaging of the deposits and/or the episodic deposition of assemblages are well known (see Appendix A3; chapter 2). However, a multi-method approach allows evaluation of exactly what each method is informing on, how these methods can be complementarily combined, and understanding why differential palaeovegetation signals may arise. Thereby, allowing these issues to be overcome and more robust conclusions to be drawn, allowing even a small dataset to inform at a greater resolution. By considering a select few individuals for which all methods were used, one can pick apart the individual ecology to form a lifetime palaeodietary, and by inference, palaeovegetation, signal. The benefit of this is to highlight the reasoning behind differential signals, i.e. whether they are due to the presence of

different populations across a long time-span or that the methods implemented are reflective of different individual animal lifetime dietary changes.

Scale

Another aspect worth considering is the scale reflected by each methodological approach (e.g. Davis & Pineda-Munoz 2016).

When used in conjunction, methods complement one another to provide a holistic lifetime and evolutionary reconstruction of diet. When used in isolation, methods may yield perceived incongruences, by recording diet over different timescales (Davis & Pineda-Munoz 2016). Dental morphology reflects the lifespan of the individual, as well as deeper evolutionary phylogenetic history of the species, genus and lineage. Mesowear represents the lifetime diet but takes at least 6 months to establish (Ackermans et al. 2018). In contrast isotopes and microwear signals reflect much shorter timescales. Isotopes reflect the early years dietary signal, laid down over a period of months-years, and the microwear signal is immediately established on the dentition but can be quickly overwritten, therefore reflects on the items consumed over the last few days/ weeks of life.

Indeed, methods such as mesowear are more fruitful when used in conjunction with other methodologies, as a broad dietary indicator (i.e. 'herbivore vs. grazer'). For example, Jones & DeSantis's (2017) multi-method approach to determining the dietary ecology of the La Brea herbivores analysed the degree to which each proxy method correlates with one another. They found that anisotropy (DMTA: *epLsar*) negatively correlated to dental occlusal relief values (mesowear) but positively with mesowear scores (scores of 0-6, 6 representing low relief, blunt cusps). This would be expected of a grazer, to have a more anisotropic dental facet and low relief with blunt cusps but the negative correlation of relief would be unexpected. Yet the higher relief could reflect lower abrasion and, or higher precipitation (e.g. Kaiser and Schulz 2006). DMTA heterogeneity was also found to have a negative correlation with mesowear scores (Jones and DeSantis 2017).

11.2 MATERIALS

Further to the materials and methods outlined for each individual method in chapter 4, the following specimens (for which more 2 or more methods were implemented) were used for the first part of this analysis (individual analysis):

Swartkrans: SKX 10697, SKX 4842, SKX 10703, SKX 11602, SK 5882, SK 5990, SK 10555, SK4064, SK 6118, SK 4083, SK 4080, SK 2292, SK 4633, SK 11899, SK 6106, SK11073, SK14070, SK 5958, SK 2953, SK 3055, SK 2366, SK 2264, SK 3014, SK 14123, SK 4054, SK 4081, SKX36545/36544, SKX 35326, SKX 33839, SKX 28999, SKX 34249, SKX 28008.

With the addition of published isotope results for *Antidorcas*, the following specimens were able to be added to the multivariate statistics, analysed for individual lifetime variation. From these individuals, only SKX 12067 also had corresponding microwear data from this study.

Sterkfontein Member 4: STS 1125, STS 1435, STS 2369, STS 1944, STS 1325A; Sterkfontein Member 5 East: S94-6124, BP/3/16974; Sterkfontein Member 5 West: S94-7314, S94-7958; Swartkrans Member 1 LB: SKX 12067.

Subsequently, the entire dataset (trends obtained via each species, per Member, ordered chronologically through time) was evaluated by combining results from all methods, as analysed in the preceding chapters.

11.3 METHODS

Scatter plots of all variable pairwise combinations were made for a visual assessment of the variables and their relationships to one another. This was done for all *Antidorcas* species for all provenance to see the general correlations between variables. Subsequently, the data was broken down by provenance (site and member) and again by species. From this assessment, visible trends could be investigated further for selected statistical analyses.

Spearman's rho correlations were made, pairwise, for each variable used to assess the contribution of variables to one another. Where correlations exist, further analysis is conducted to test if this correlation persists through time (i.e. if the correlation is apparent in each member) and for each species.

11.4 RESULTS

11.4.1 Individual *Antidorcas* comparison across methods

A selection of *Antidorcas* individuals with at least two methodological data results available are presented here to evaluate the dietary signal achievable from one individual and to test if that signal prevails regardless of method applied and throughout the lifetime of the individual animal. I.e. are they mixed feeding individuals, seasonal mixed-feeding individuals or mixed-feeders collectively as a species, with the species supporting habitual grazers and habitual browsers.

Correlations

Variables from different methods showing correlations (Table 11.1:) are explored further here and see Appendix A9.

Spearman's rho correlation of all variables

Table 11.1: Spearman's rho pairwise correlations of all variables used. Positive correlations are shown above the line and negative correlations are shown below the line. Strong correlation=bold text (+1 to+0.5/-0.5 to -1), weak correlation=normal text (+0.5 to 0/ 0 to –0.5). Significance is indicated here by the number in the box ('0' shows p<.000). Acronyms are described in detail in chapter 4, for each method used. Measurements: 'MDL'=mesio-distal length, 'BLW'=bucco-lingual width, 'CH'=crown height, 'OH'=occlusal height, 'TH'=total height, 'EA/EB/EC/ED'=enamel thickness at locations A,B,C, and D. Mesowear: 'MS 1-6'=Mesowear score (1-6), 'RLF'=occlusal relief, 'CS'=cusp shape, 'NMWS'=new mesowear score (1-49). DMTA: 'Asfc'= area scale fractal analysis, 'R^2'=angle of the slope, 'Smc'=scale of maximum complexity 'StDvn'= standard deviation, 'epLsar'= length-scale anisotropy of relief; 'HAsfc'=heterogeneity of area scale fractal complexity (at scales 9 and 81), 'TfV'=textural fill volume. Isotopes: 'δ13C'=carbon isotopes, 'δ18O'=oxygen isotopes.

	MDL	BLW	CH	OH	TH	EA	EB	EC	ED	MS 1-6	RLF	CS	NMWS	Asfc	R^2	Smc	StDvn	epLsar	HAsfc 9	HAsfc 81	TFV	δ13C	δ18O
MDL				0.012	0.13														0.004	0.035			
BLW																		0.02			**0.009**		
CH		0.048		0.005			0.031			0.006	0.001		0										
OH					0.002		0.014	0.001		**0**	**0**	0.003	**0**			0.021						0.022	0.023
TH										0.026			0.016	0.042			**0.003**					0.02	
EA			0.02		**0**			0.001														0.011	0.047
EB										0.022	**0**											**0.002**	**0.007**
EC											0.029		0.024									0.016	0.001
ED			**0.023**															**0.039**			**0.008**		
MS 1-6											**0**	**0**	**0**		0.007	0.009	0.032						
RLF												0	**0**		0.011								
CS													**0**		0.016	0.002	0.023						
NMWS		0.047													0.033	0.002							
Asfc																	**0**				0.05		
R^2									**0.008**							0.002							
Smc																	0.025	0.038					
StDvn																							
epLsar																							
HAsfc 9				**0**		**0.003**	**0.017**			**0**	**0**	**0**	**0**	**0**		0.036		0.009		**0**			
HAsfc 81				0.042						0.001	0.002	0.006	**0.001**	0.038									
TFV										0.006	0.001	0.036	0.017	0.014								0.009	0.018
δ13C																		0.011					0.02
δ18O					0.013																		

Stable isotopes and enamel thickness

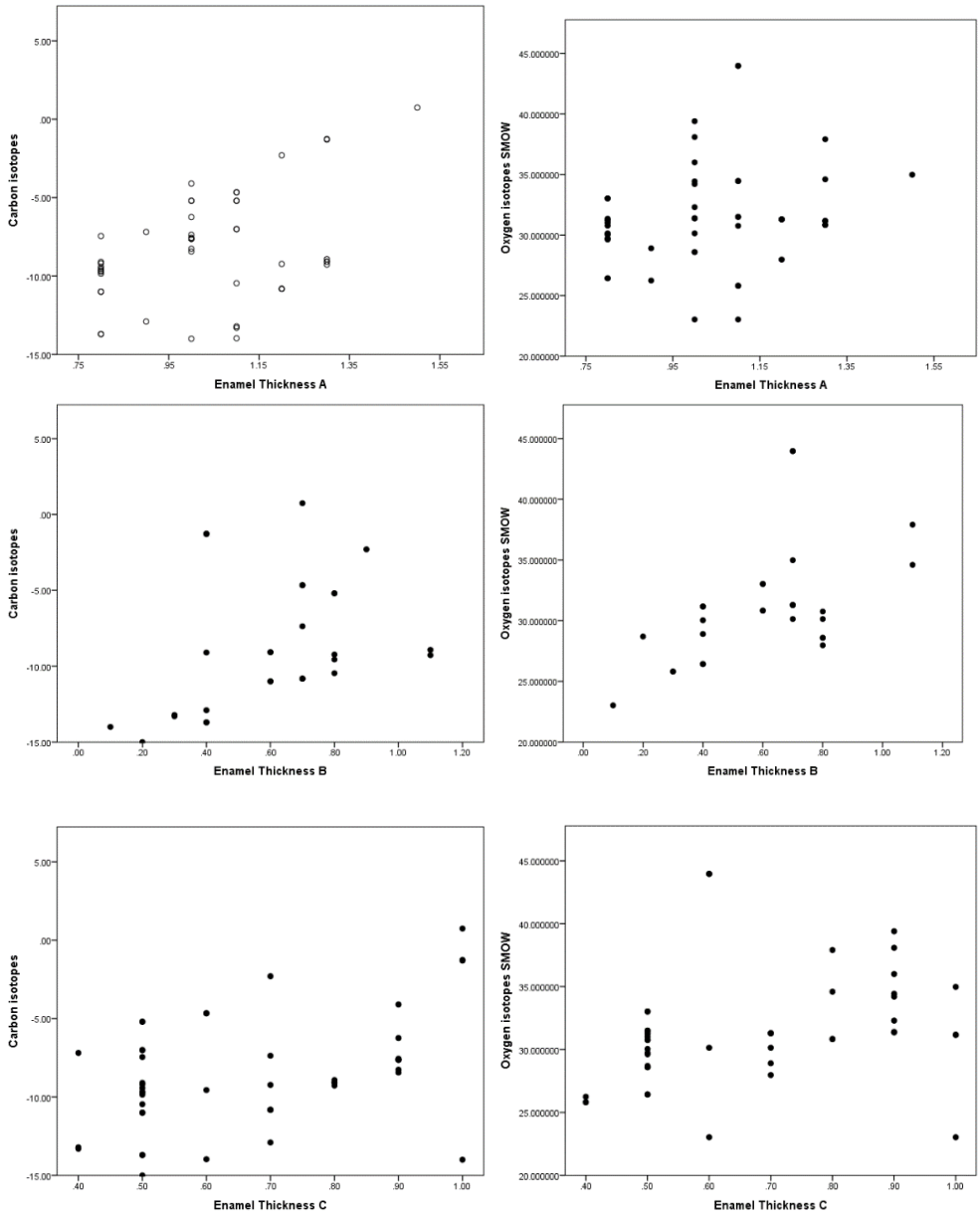


Figure 11.1: Scatter plot showing individual Antidorcas specimens carbon isotope $\delta^{13}C$ (‰) values on the Y axis (left side plots) and oxygen isotope $\delta^{18}O$ (‰) values on the Y axis (right side plots), compared to enamel thickness at measured locales (A-C) (in mm) on the X axis. The overall correlation (rather than specific values) are important here.

A positive correlation was observed for both carbon and oxygen isotopes against enamel thickness (weak positive for enamel thickness at locations 'A', 'C' and 'D' and a strong positive correlation at location 'B'). This was investigated further, separating the dataset by tooth type to determine if the trend between enamel thickness and isotopes varied across the toothrow (see Appendix A9). When separated out, sample sizes were very small, typically lower than n=10. Due to small sample sizes, caution is exercised for any observed patterns (i.e. these patterns should only be used in support of studies with similar findings, rather than stand-

alone evidence, hence these graphs are included only in the appendices). To attempt to corroborate this trend, further analysis was carried out.

Further Analysis

From a spearman's rho correlation for only the *Antidorcas* with both enamel thickness measurements and stable oxygen isotope values (n=14), a correlation exists between $\delta^{18}O$ and enamel thickness (p=.049). However, when the dataset is split by member (Time), no correlation exists. The same is true for splitting the dataset by species. This trend is also observed for carbon isotope value against enamel thickness (p=.015), again this trend is not seen when split but member, or by species. Carbon isotope values are more species (dietary)-dependent, making this correlation of relatively little value.

When broken down by tooth type, this trend was only prevalent for the lower second molar for enamel thickness A. [For lm_2, enamel thickness A represents the buccal enamel surface, B the interior facet and C the lingual enamel surface (D is not present)]. The opposite trend exists for the upper second molar than is true for the other molars. The same is true for enamel thickness D (mesostyle) (Table 11.1).

The significant findings here are summarised below, however, larger sample sizes are required taking this further and is an avenue for future research.

Enamel thickness, taken as a mean from all locations (see chapters 4 & 7) produces these significant correlations, as does enamel thickness at locations A and B (but at locations C and D, these correlations are not present). A Spearman's rho correlation revealed strong, positive correlations for the following:

Table 11.2: Significant correlations for enamel thickness and stable isotopes. 'N' = number of individuals, 'EA' is representative of the buccal enamel band, 'EB' of the central enamel band, p=significance value.

Molar	N	Correlating variables		P	Correlation coefficient
		Enamel Thickness	Isotope		
Lower	8	EA	$\delta^{13}C$	.014	+0.814
Lower	8	EA	$\delta^{18}O$	.020	+0.790
Lower	7	EB	$\delta^{18}O$	.025	+0.815
Upper	6	EB	$\delta^{13}C$	.036	+0.841

If this trend prevails with larger sample sizes, climate could be correlated as an evolutionary driver of dentition. This trend could reflect aridity as an evolutionary driver for dentition, to withstand adaptive forces potentially caused by climate-induced vegetation changes (enamel thickness) and linked to aridity levels ($\delta^{18}O$). Although yet another step removed, as an ongoing debate exists regarding the adaptive drivers of differential dentition and their implications for *Paranthropus* and *Australopithecus* (e.g. Grine 1986; Skinner et al. 2008, 2009; Rabenold and Pearson 2011), climatically-driven dental adaptations could provide key insights into evolutionary drivers in many species, even hominins. Especially if, as *Antidorcas*, both species were dietary, habitat and ecological generalists (e.g. de Ruiter 2008b; Wood and Strait 2004).

DMTA and Mesowear

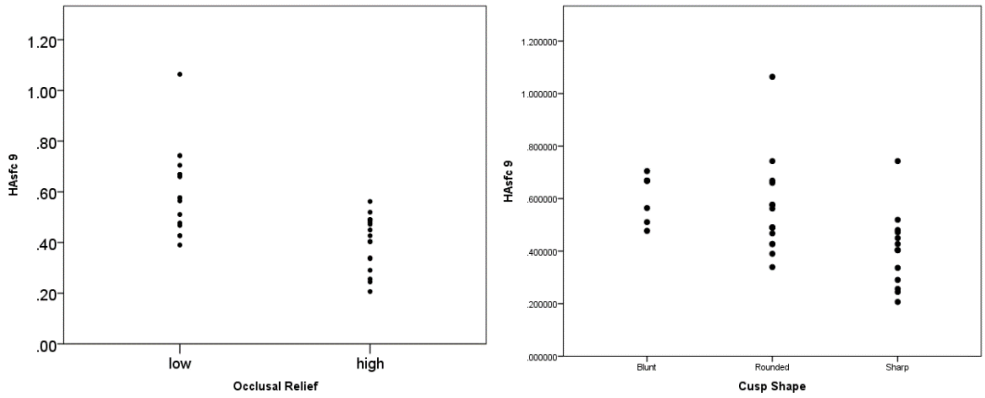


Figure 11.2: Scatterplot showing individual Antidorcas specimens dental occlusal relief (mesowear) on the x-axis (left) and cusps shape (mesowear, blunt on the left nearest the origin, to rounded and sharp to the right) on the x-axis (right) against heterogeneity (HAsfc 9cell) (μm) on the y-axis. The overall correlation is of importance (rather than individual values).

A negative correlation exists between HAsfc[9] and occlusal relief, i.e. as relief increases, heterogeneity decreases. Figure 11.2 shows the negative correlation between heterogeneity (DMTA) and occlusal relief (mesowear) on the left and between heterogeneity (DMTA) and cusp shape (mesowear) on the right, for *Antidorcas* for all members combined. The opposite would be expected, with browsing species typically displaying high relief and greater heterogeneity, whilst grazers tend towards lower occlusal relief with more homogeneity in their wear patterns. The same is true for cusp shape, displaying a negative correlation to heterogeneity.

When the dataset is split by provenance, this trend is only computable (due to requiring a sufficient sample size), and prevalent for Swartkrans Member 2. When split by species, within Swartkrans Member 2, this negative correlation between heterogeneity and occlusal relief exists moderately for *A. marsupialis* (significance=.043; correlation coefficient=-.547 (; n=14) and strongly for *Antidorcas* sp. (significance=.000; correlation coefficient=-.869; n=15). No correlation exists for *A. bondi* (n=9). The negative correlation between heterogeneity and cusp shape exists only for *Antidorcas* sp. (significance=.000; correlation coefficient=-.815; n=15) this correlation is strong, yet *A. marsupialis* and *A. bondi* do not display the same correlation between heterogeneity and cusp shape.

This correlation exists for both M^2 (significance=.024; correlation coefficient=-.671; n=11) and M^3 (significance=.012; correlation coefficient=-.514; n=23) unfortunately, sample sizes were too small to assess this correlation for other tooth types.

This unexpected correlation suggests that the mesowear variables are not as clearly defined as the current literature suggests. There are more factors to consider than simply a 'grazing' and 'browsing' expected mesowear signal and the parameters of the mesowear method require reassessment.

If accepting the current mesowear parameters, it is possible that a high level of abrasion, (inflicting long term selection pressure, such as increased crown height) is also responsible for high levels of overwriting of microwear signals. Higher levels of abrasion increase overwriting

of previous microwear scars, reducing the timeframe represented by microwear. This may produce a 'false' low heterogeneity for the browsing individuals due to only short-term preservation of wear from masticated vegetation. As these individuals display high relief and sharp cusps and tend to show browsing isotope signals, it is likely that they were not wearing their teeth down (which should result in lower relief and rounded-blunted cusps) from grass phytoliths, instead it is possible that this suspected abrasion come from exogenous particles, such as dust.

A weak positive correlation was observed between oxygen isotope values and Tfv values (Figure 11.3), supporting dietary flexibility (high Tfv) in relation to increased aridity and / or increased leaf consumption ($\delta^{18}O$).

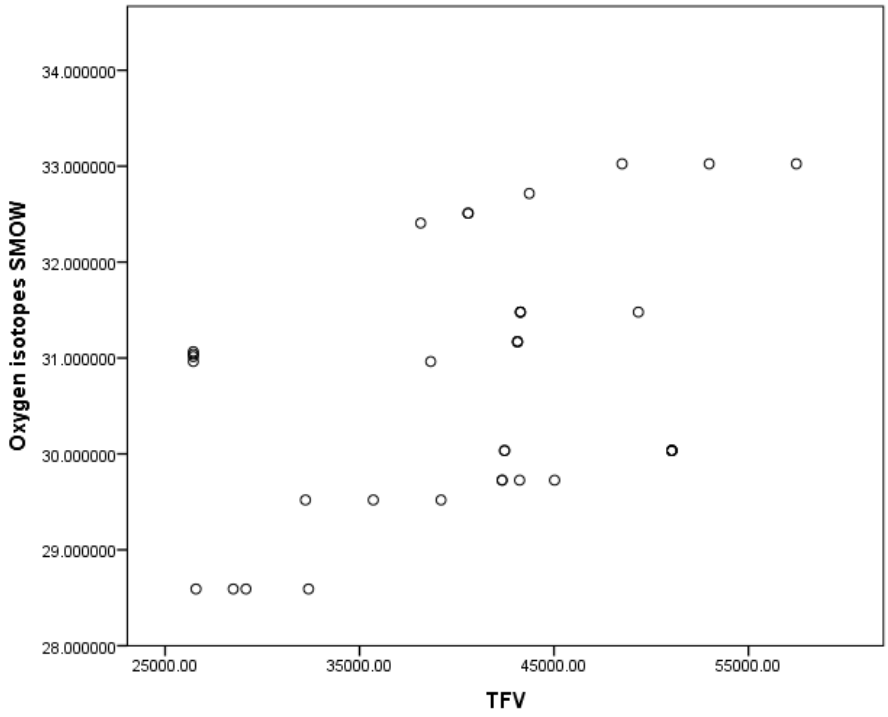


Figure 11.3: Scatter plot showing Oxygen isotope $\delta^{18}O$ (‰) values on the Y axis, against Tfv (DMTA) values (μm) on the X axis.

There was no correlation observed between carbon isotope values and mesowear cusp shape (Figure 11.4) for *Antidorcas*. This scatter plot does however, show the dominance of rounded cusps (suggesting an abrasive element is common in the diet) and a hint of clustering of $\delta^{13}C$ values as mixed-feeding (-5 to -9‰), to browsing (below -9‰) and grazing (above -2‰) groups. Those individuals with carbon isotope values ($\delta^{13}13$) closer to the grazing / browsing boundary being perceived as having more variable diets, these clustering are indicated in (Figure 11.4). There is a marginal tendency for mixed-feeders-grazers (above -9‰) and grazers (above-2‰) to display blunt cusps and for mixed-feeders-browsers (below -5‰) and browsers (below -9‰) to tend towards sharp cusps.

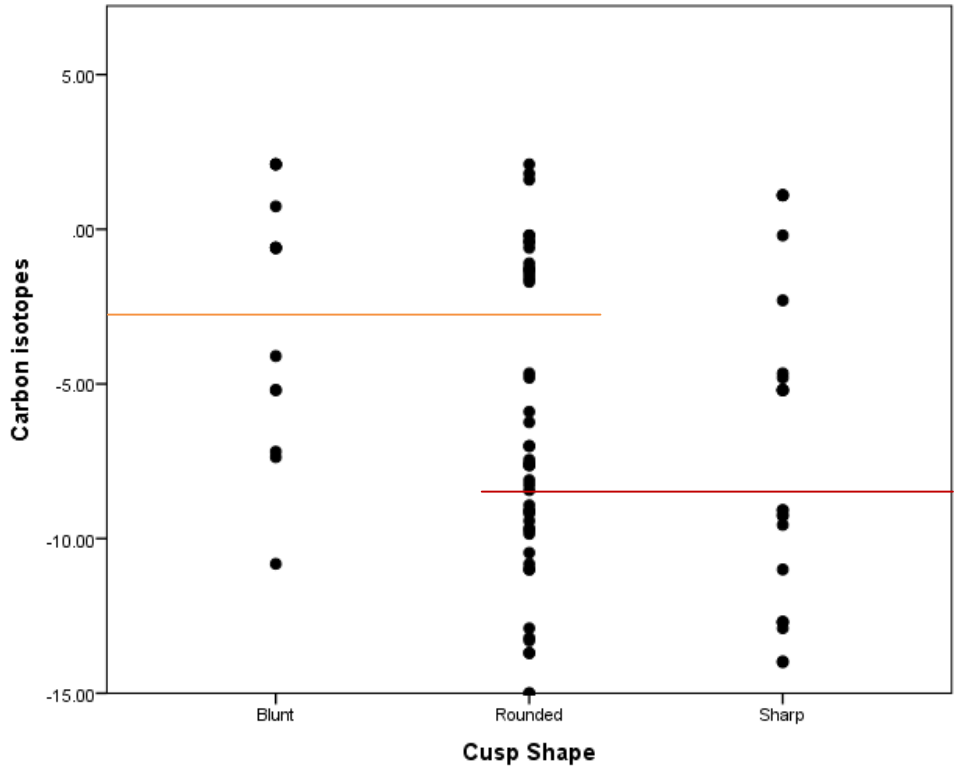


Figure 11.4: Scatter plot showing individual Antidorcas specimens molar cusp shape (mesowear) on the x-axis against carbon isotope value $\delta^{13}C$ (‰) on the Y-axis. Above the green line on the left indicates predominantly grazing diets, below the red line on the right indicates predominantly browsing diets. Mixed feeding diets are those that fall within the other areas, particularly central to grazing/browsing.

DMTA, isotopes and enamel thickness

No correlation was seen for microwear and enamel thickness, which may be expected as microwear may not reflect lifetime dietary preferences and therefore does not represent the adaptive force acting on the dentition. The idea that the animals may not have been eating their preferred diet leading up to their death is supported by a lack of correlation between most microwear values and carbon or oxygen isotopes. The only, albeit weak, trend observed is between oxygen isotopes and Tfv. Of all the microwear variables, Tfv is likely to show longer term dietary preferences, *if* overwriting from the most recent meals does not mask the signal. Deeper and /or larger pits and scratches are less likely to be overwritten where the last few meals are of softer food particles (e.g. fine grasses with few silica bodies or phytoliths).

Looking at the individual values: Tfv compared to Smc (the scale at which the wear signal is obtained and shows the most complexity), the higher Tfv values are often taken at a higher scale. The very highest values for Tfv are also for Smc but there are not always consistently high Tfv and high Smc values.

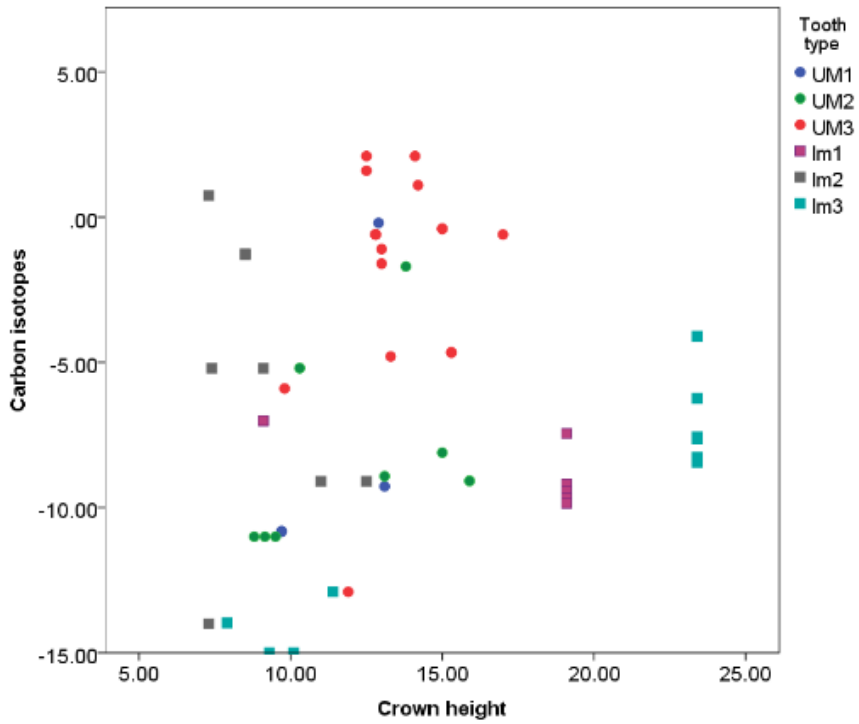


Figure 11.5: Scatter plot showing individual Antidorcas specimens dental crown height in mm (x axis) against carbon isotope value $\delta^{13}C$ (‰) on the Y-axis. A weak positive correlation was found for all tooth types (individually and combined), all tooth types are shown on this graph.

A weak positive correlation was found between crown height and carbon isotope $\delta^{13}C$ (‰) values (Figure 11.5) and oxygen isotope $\delta^{18}O$ (‰) values (Figure 11.6). As expected, individuals with a browsing isotope signal (low $\delta^{13}C$), have lower crown heights. More abrasive diets (typically grazing) are likely to result in selection for taller crowns as a structural mechanism to withstand the abrasive pressure. Although a weak positive trend was also shown for crown height against oxygen isotope values, considerable variation was apparent between tooth types (Figure 11.6). This is possibly due to oxygen isotope values reflecting palaeoenvironmental complexities beyond dietary parameters. The same is true for occlusal height and isotope values. A weak positive correlation was also found for occlusal height and carbon $\delta^{13}C$ (‰) (Figure 11.7) and oxygen $\delta^{18}O$ (‰) (

Figure 11.8:) isotope values.

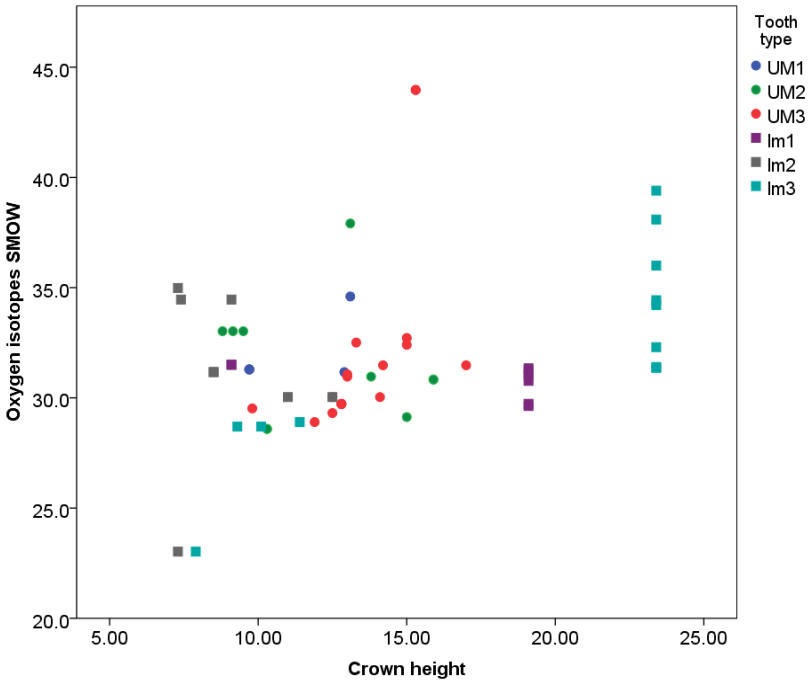


Figure 11.6: Scatter plot showing individual Antidorcas specimens dental crown height in mm (x axis) against oxygen isotope value $\delta^{18}O$ (‰) on the Y-axis. A weak positive correlation was found for all tooth types (individually and combined), all tooth types are shown on this graph.

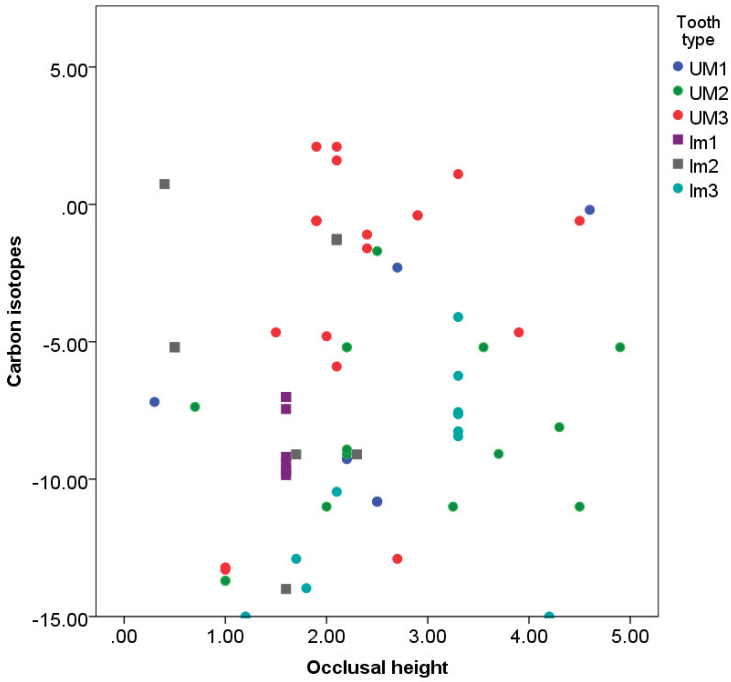


Figure 11.7: Scatter plot showing individual Antidorcas specimens dental occlusal height in mm (x axis) against carbon isotope value $\delta^{13}C$ (‰) on the Y-axis.

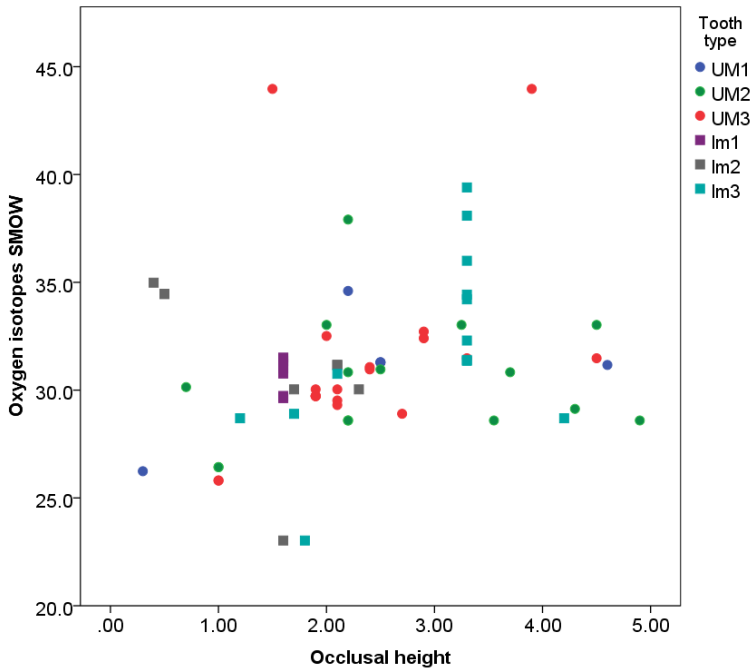


Figure 11.8: Scatter plot showing individual Antidorcas specimens dental crown height in mm (x axis) against oxygen isotope value $\delta^{18}O$ (‰) on the Y-axis.

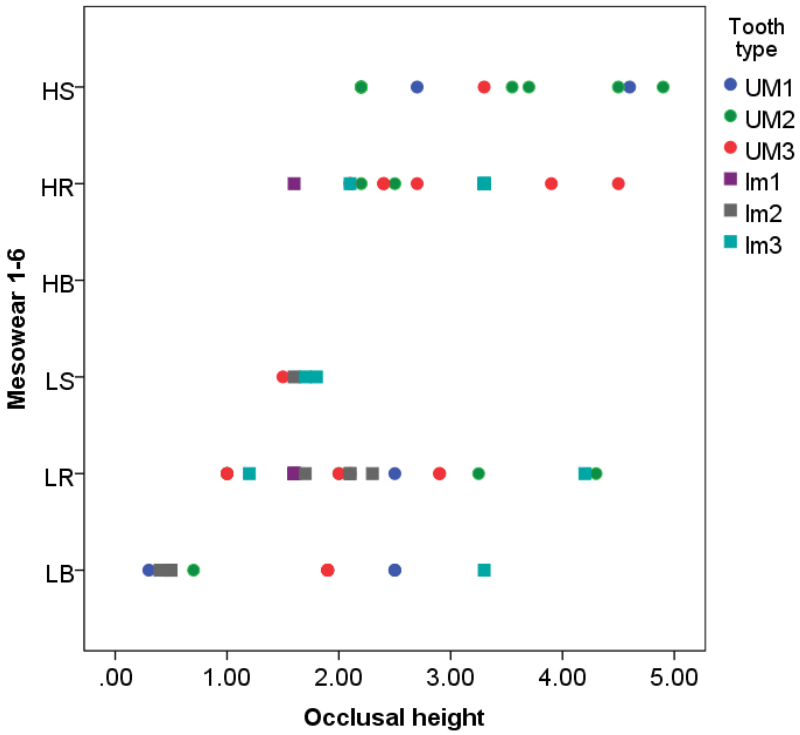


Figure 11.9: Scatter plot of Antidorcas dental occlusal height (in mm) on the x axis against Mesowear score on the y axis. Mesowear scores from LB (score 1, low relief and blunt cusps) to HS (score 6) are stated on the axis.

A strong positive correlation between occlusal height and mesowear score was found for *Antidorcas* dentition (Figure 11.9). This correlation was expected as lower occlusal heights (physical measurements of cusps) are associated with an abrasive diet, as are lower mesowear scores (which includes the relative cusp relief, inherently linked to occlusal heights). Figure 11.9 may hint at a possible plasticity to teeth beyond what would be expected. However, the impact of time-averaging is probable here. That is, it is not possible to determine the impact on individuals' lifetime scale to assess response (to abrasion versus attrition of diet as represented by mesowear) plasticity.

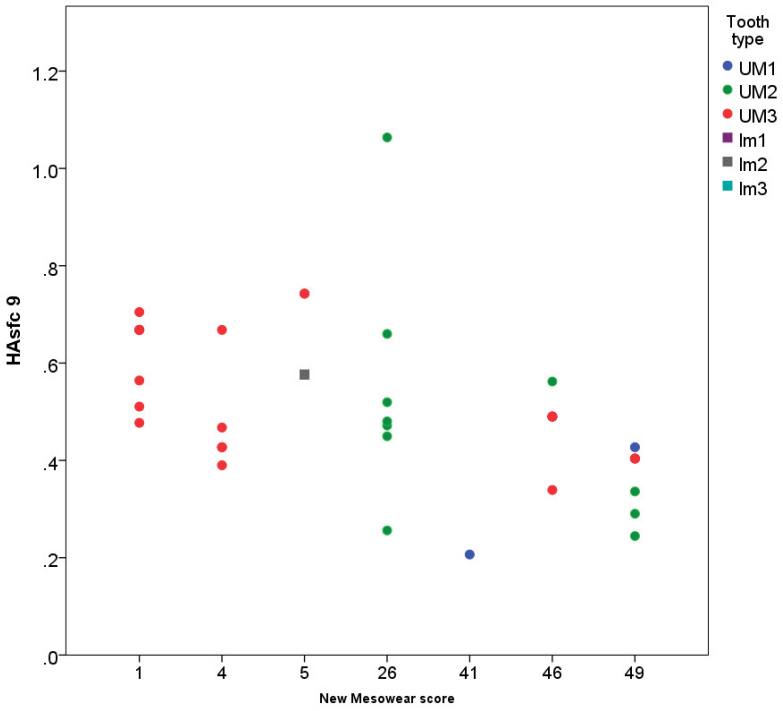


Figure 11.10: Individual Antidorcas new mesowear scores (continuous scale 1-49) on the x axis showing a strong negative correlation against dietary heterogeneity HAsfc 9cell (µm).

A strong negative correlation exists between heterogeneity (HAsfc) of diet and continuous mesowear scores (

Figure 11.10 and Figure 11.11). This is opposite to what may be anticipated, as browsers are thought to have high relief and sharp cusps (higher mesowear score HS=49 (new mesowear scores) or HS=6 (mesowear score), see chapter 8 'Mesowear') and relatively high heterogeneity evidenced via microwear analysis. Mixed feeders typically have the highest microwear heterogeneity. This may be skewed by age of individuals. Younger individuals, with lower levels of lifetime wear (and less time to display mesowear signatures, see Ackermans et al. 2018) are also less likely to have high microwear heterogeneity. Although microwear primarily indicates the last few meals, these are being imprinted on top of existing microwear patterns.

Where fewer microwear scars have been impressed on the dental enamel in younger individuals, their heterogeneity is likely to present as lower. This correlation could also/ alternatively represent abrasive mixed feeding dietary practices.

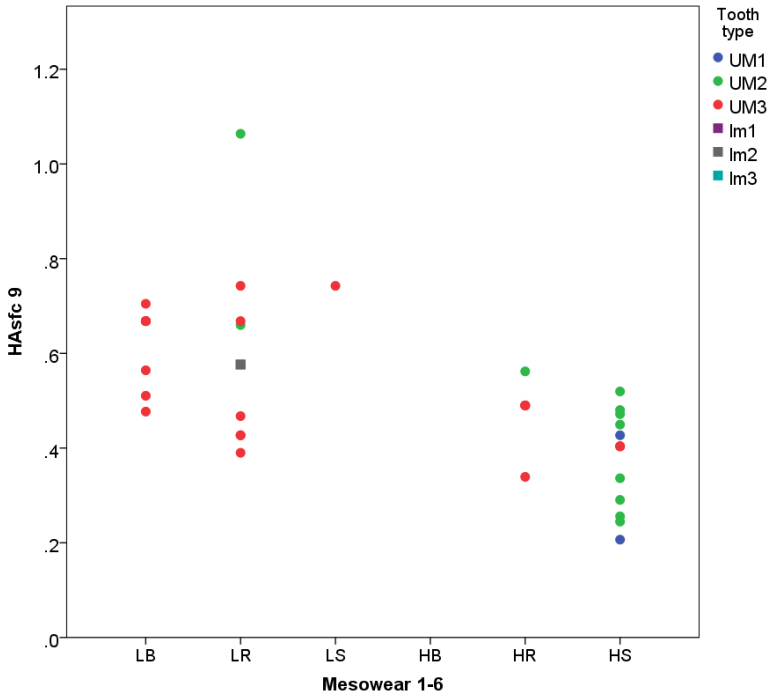


Figure 11.11: Scatterplot showing Individual Antidorcas mesowear scores (continuous scale 1-6) on the x axis showing a strong negative correlation against dietary heterogeneity HAsfc 9cell (μm).

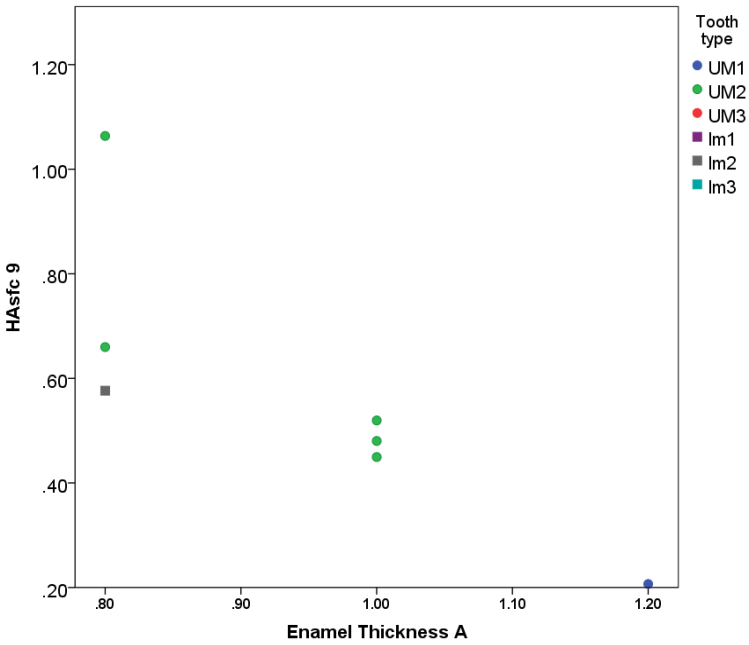


Figure 11.12: Scatterplot showing Individual Antidorcas enamel thickness A (in mm) correlated against heterogeneity of microwear (HAsfc9cell, in µm).

The strong negative correlations between heterogeneity ($HAsfc^9$) and enamel thickness (location A and B, see chapter 7 'Measurements') (Figure 11.12-Figure 11.13) supports a selective pressure on the molars due to an abrasive diet. Homogenous (typically grazing) diets are more abrasive, selecting for structural reinforcements for greater enamel thickness. That these correlations exist, suggest that the microwear signals are not indicative of fall-back foods primarily but those that are often consumed for a sufficiently long duration within the life to select for masticatory adaptations to support these dietary practices.

In contrast to heterogeneity (Figure 11.13), a strong positive correlation between inner enamel thickness ('EB' see chapter 7 'Measurements') and occlusal relief (see chapter 8 'Mesowear') was found (Figure 11.14). The opposite may be expected, however, this correlation could be a sampling artefact, either due to sample size or, reflect younger individuals. Younger individuals would display higher relief due to the shortage of duration of life within which to wear the relief down by vegetation consumed. The inner enamel is also thicker due to lack of wear. Care was taken to avoid obviously very young or very old individuals but this possibility cannot be completely ruled out. Alternatively, the inner enamel and outer tooth edge (relief is measured on the outer tooth edge) could be interacting with the vegetation and wider environmental influences in slightly differing ways. Further analysis with larger sample sizes would be required to test this.

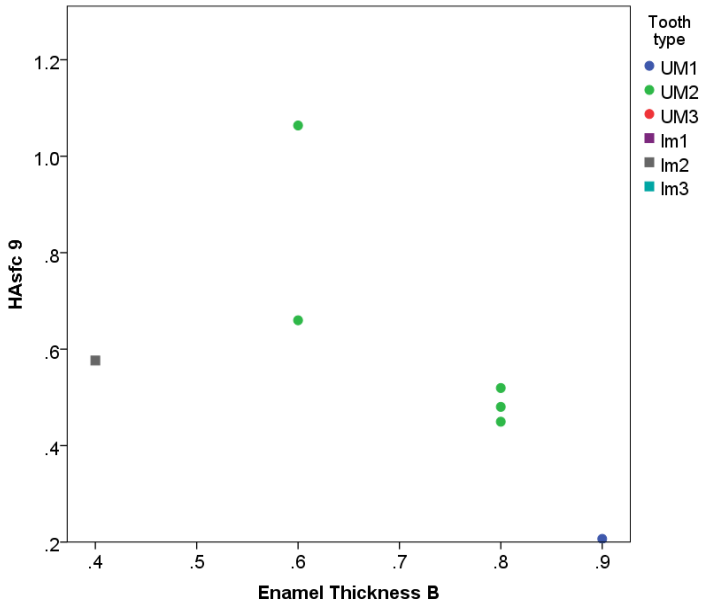


Figure 11.13: Scatter plot for Antidorcas inner enamel thickness (in mm, location B, see chapter 9, 'Measurements') on the x axis against diet heterogeneity (HAsfc[9] µm) on the y axis.

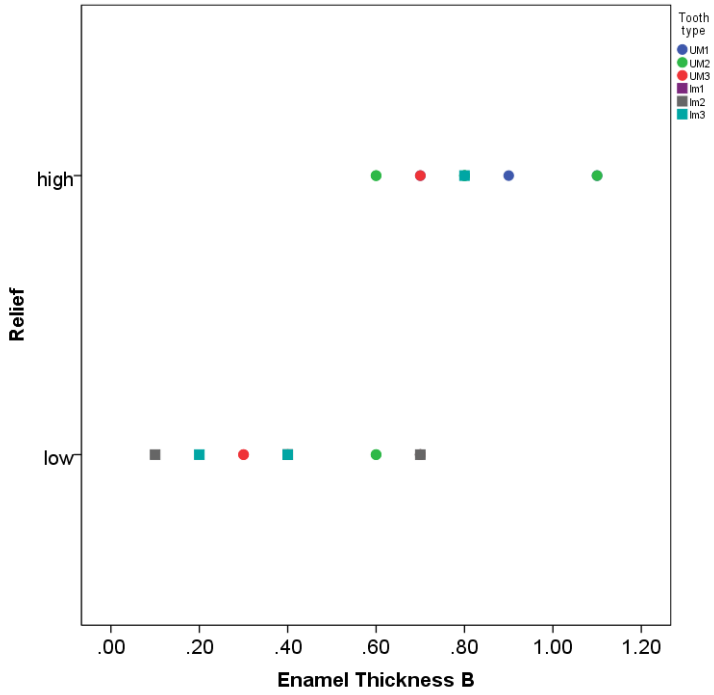


Figure 11.14: Scatter plot showing the correlation between Antidorcas dental enamel thickness of the molar infundibulum (inner enamel band) (in mm) and occlusal relief (high / low).

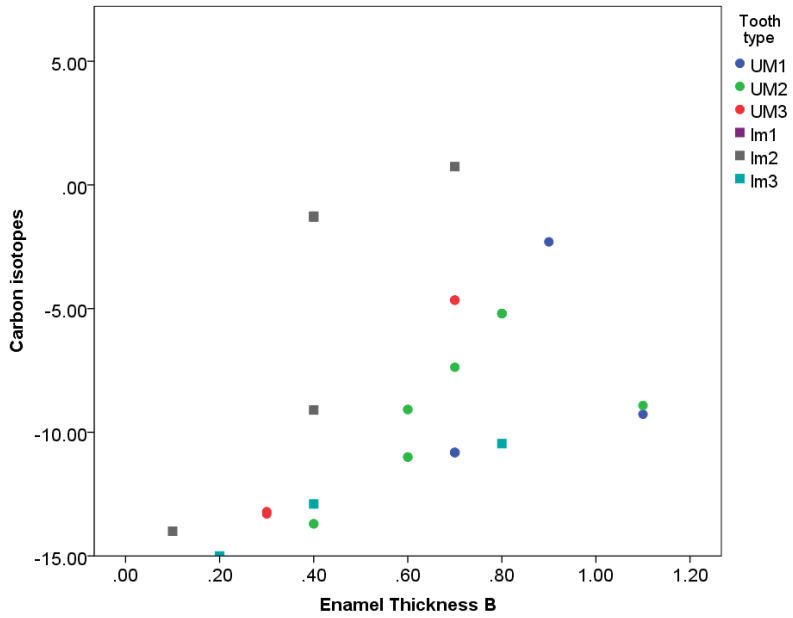


Figure 11.15: Scatter plot showing the correlation between Antidorcas dental enamel thickness of the molar infundibulum (inner enamel band) (in mm) and carbon isotope $\delta^{13}C$ (‰) values.

Figure 11.15 and Figure 11.16 ‘s correlations, introduced earlier (and see Appendix A9) explore inner enamel thickness correlations in one combined plot, whilst still differentiating between tooth type. This is to place this correlation with the sequence of considering the inner enamel, which appears to show many correlations to other dietary variables (Figure 11.13-Figure 11.16). Figure 11.15 displays the potential relationship between diet ($\delta^{13}C$) and the selection pressure this diet may exert on inner enamel thickness.

These correlations (Figure 11.13-Figure 11.16) can be linked to the inner mesowear scores (Mesowear III). Exploring these correlations further with the input of the mesowear III scores with larger sample sizes is an avenue for future research. Here, the correlations support increased inner enamel thickness to withstand abrasive, homogenous (HAsfc) diets. Abrasive mixed feeding diets are suggested due to the strong negative correlation between carbon isotopes ($\delta^{13}C$) and enamel thickness.

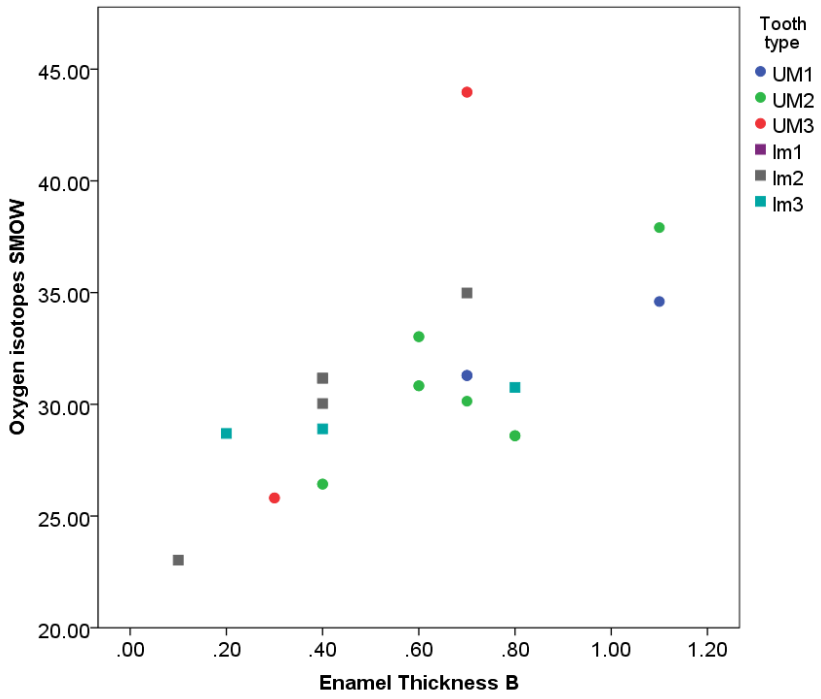


Figure 11.16: Scatter plot showing the correlation between Antidorcas dental enamel thickness of the molar infundibulum (inner enamel band) (in mm) and oxygen isotope $\delta^{18}O$ (‰) values.

A strong positive correlation between bucco-lingual width and textural fill volume of microwear scarring may implicate the material properties of the vegetation consumed. This trend (Figure 11.17) is not an artefact of species molar size differences as it prevailed for *A. bondi*, *A. marsupialis* and *Antidorcas* sp. (specimens only identified to genus level), no *A. recki* specimens with both variables were present in the dataset, so the correlation for *A. recki* could not be established.

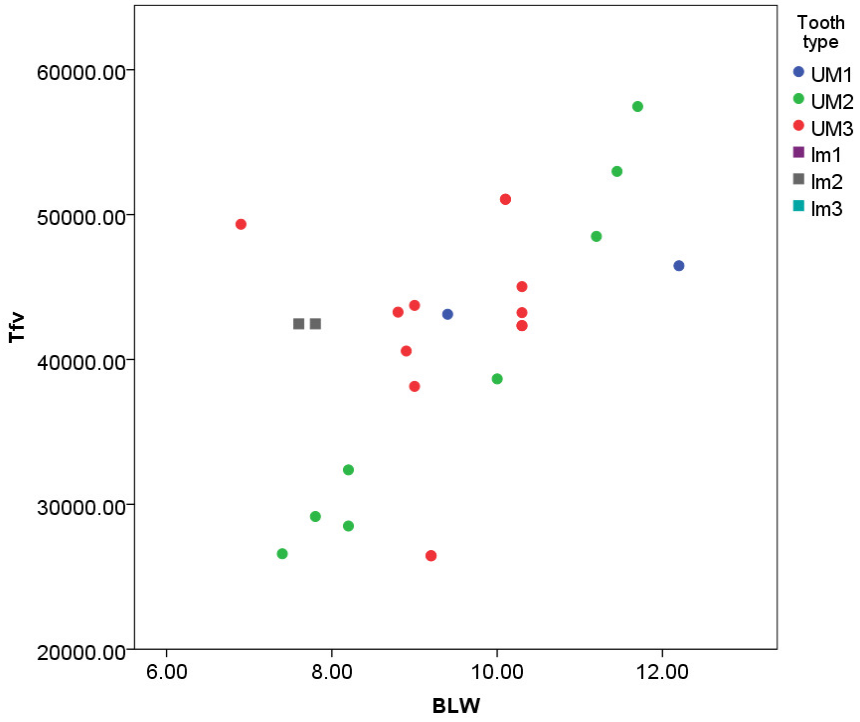


Figure 11.17: Scatter plot showing the correlation between Antidorcas bucco-lingual width (BLW, in mm) against Textural fill volume (Tfv) of dental microwear (in µm).

The strong positive correlations between enamel thickness on molar mesostyles (enamel thickness D, see chapters 4 &7) and complexity (epLsar) and textural fill volume (Tfv) (Table 11.1) supports an interpretation of mixed feeding, yet abrasive diets. The enamel thickness responds on a longer time scale through selective pressure, the microwear (epLsar and Tfv) reflect the last few days/ weeks dietary indications. The selection could therefore, be a result of seasonal mixed feeding.

Use-wear and Stable isotopes

Data chapters 7-10 (Measurements, Mesowear, Microwear and Isotopes) suggest heightened inter- and intra-specific variability for Swartkrans Member 2. This Member is therefore explored further here by directly comparing signals from each method of dietary inference.

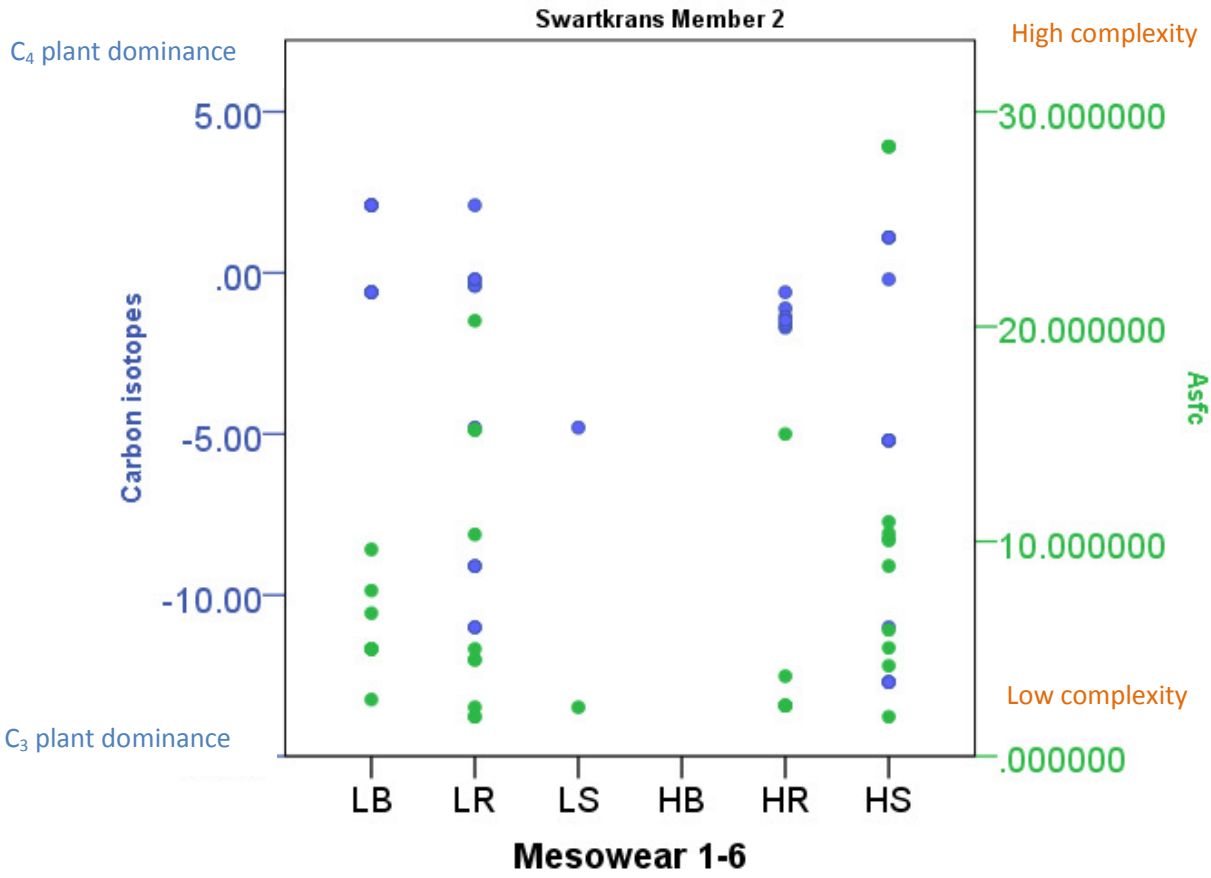


Figure 11.18: Scatter plot showing individual Antidorcas upper molars from Swartkrans Member 2 early years signal (carbon isotope $\delta^{13}C$ (‰)values) along the left hand side y-axis and indicated by blue dots, lifetime dietary signal (mesowear score) along the x-axis (indicated by green dots) and last few weeks of life (Asfc (μm) microwear signal). The green dots represent the microwear enamel surface complexity (right Y axis only) and correspond to the X axis for mesowear score. The blue dots represent carbon $\delta^{13}C$ (‰) (left Y axis only) and correspond to the X axis for mesowear score.

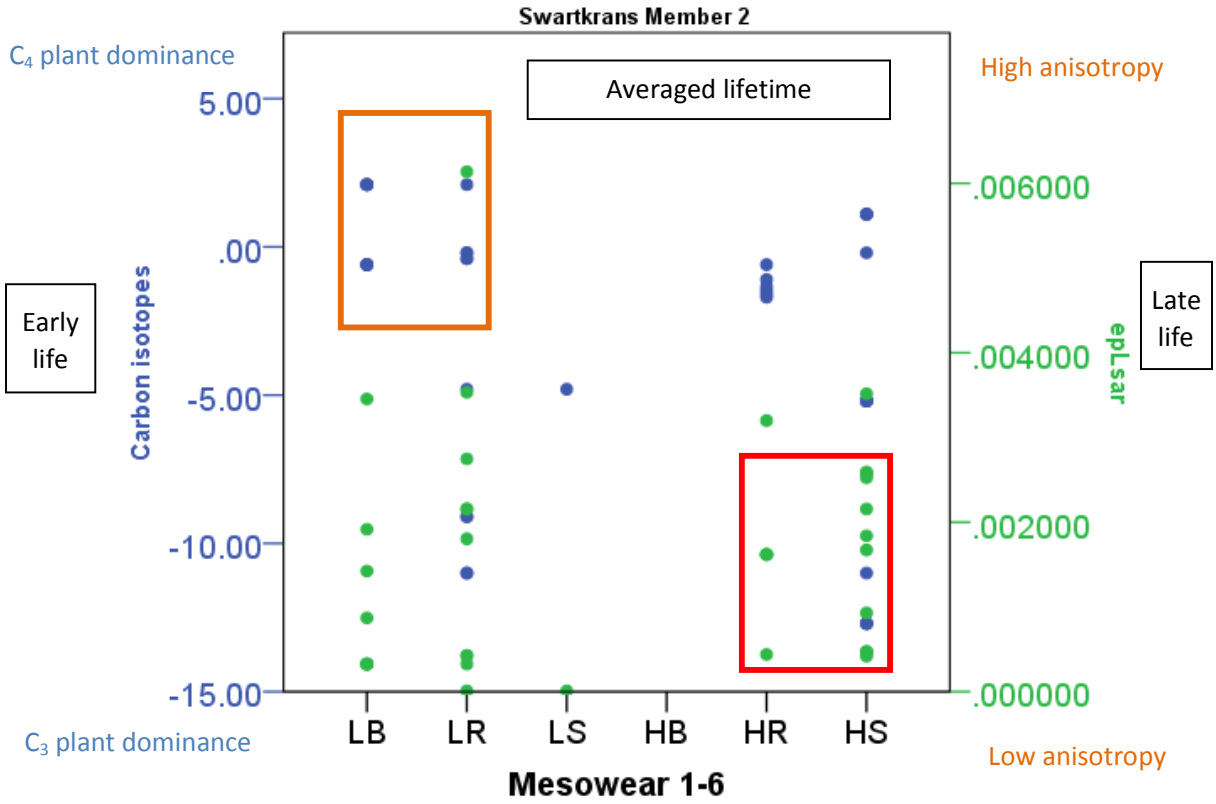


Figure 11.19: Scatter plot showing individual Antidorcas upper molars from Swartkrans Member 2 early years signal (carbon isotope $\delta^{13}C$ (‰) values) along the left hand side y-axis, lifetime dietary signal (mesowear score 1-6) along the x-axis and last few weeks of life (epLsar microwear signal). Only epLsar (μm) values (green) typical of browsing (below 0.006 μm) were present from these Antidorcas individuals in Swartkrans Member 2. The carbon isotope values (blue) show a more mixed-feeding to grazing signal. The green box indicates graze-dominated diets, the red box, browse-dominated diets.

This (Figure 11.19) is likely to show a dominance of *A. bondi* within the SKX M2 assemblage, reflecting typically grazing dietary habits, but perhaps relying on fallback foods during the temporal period of Swartkrans Member 2. Or of herd demographics, young graze, mixed-feeding diet through life and browsing due to (perhaps seasonal) availability. *Antidorcas* inter- and intra-specific variation is evident for Swartkrans Member 2. Individuals appear to be typically browsing-mixed-feeding early and late in life but not exclusively throughout their lifetime. These individual *Antidorcas* were potentially including abrasive grasses in the diet seasonally, or else incorporated other abrasive elements impacting on use-wear signatures.

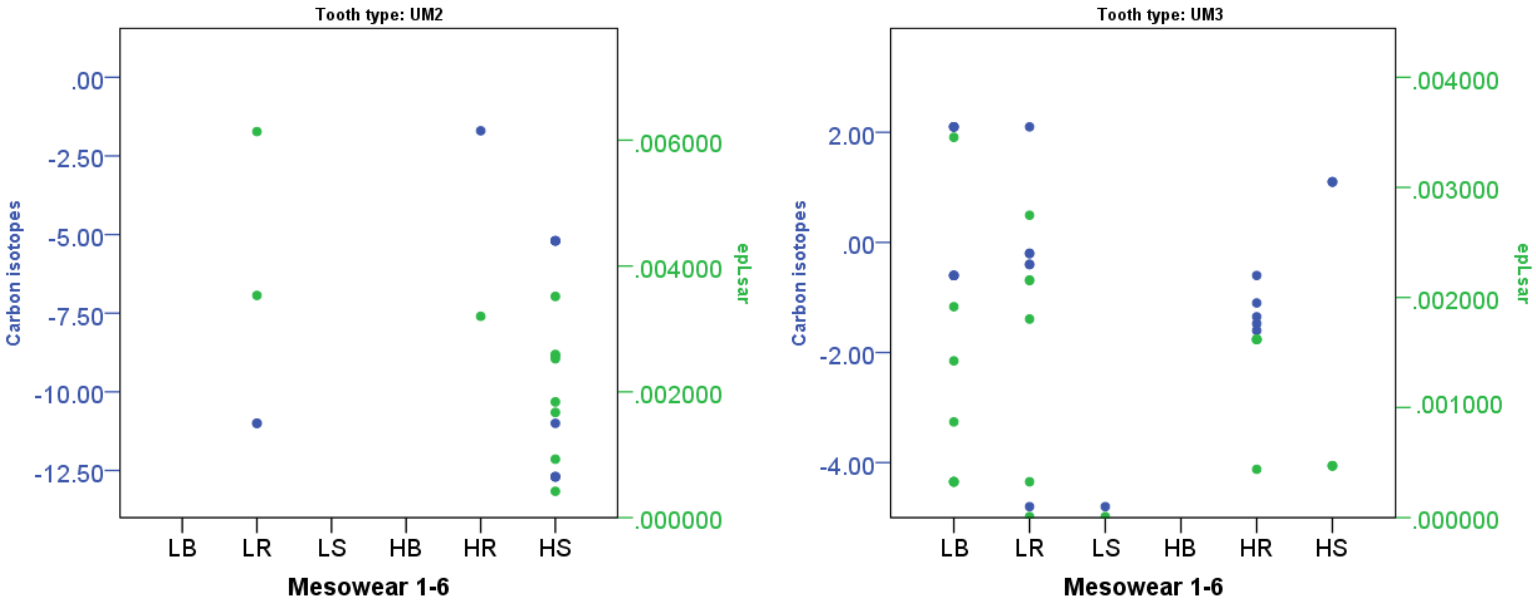


Figure 11.20: Scatter plot showing individual Antidorcas from Swartkrans Member 2 early years signal (carbon isotope $\delta^{13}C$ values) along the left hand side y-axis, lifetime dietary signal (mesowear score) along the x-axis and last few weeks of life (epLsar (in µm) microwear signal). Only epLsar values (green) typical of browsing (below 0.006 µm) were present from these Antidorcas individuals in Swartkrans Member 2. The carbon isotope values (blue) show a more mixed-feeding to grazing signal. Values are split according to tooth type (upper second molar on the left and upper third molar on the right).

Differential dietary signals along the toothrow could represent time-averaging or species-averaging rather than different teeth reflecting a conflicting dietary signal along the toothrow of the same individual i.e. tooth types being represented differentially in deposits.

From the upper second molar (left), carbon isotopes and microwear show mostly browsing signals. The dominance of HS (high relief and sharp cusps, typical of a browsing individual) support the overall browsing dominance, with some mixed-feeding. The rounding of cusps (mesowear LR/HR) suggests some degree of abrasion to the molar cusps. More C_4 vegetation inclusion is shown in the upper third molar (right) by the carbon isotopes and mesowear signal but browse-dominance is still reflected via microwear (anisotropy epLsar).

It is possible that M^3 is more susceptible to abrasive diets than M^2, however, these teeth are most likely represented by different individual animals (rather than from the same animal along the tooth row) so this cannot be conclusively tested here. (Only these two tooth types are represented by all of these methods in this dataset).

To consider signal discrepancies apparent from different tooth types, the M^3 was examined further and contrasted to the M^2 signal. As indicated in Figure 11.21 carbon isotopes show the dominance of grazing in early life (blue circles showing enriched $\delta^{13}C$ values), mixed-feeding with a relatively abrasive diet (rounding to blunted molar cusps seen via mesowear) but browsing dominates their end of life diet (green circles indicative of isotropic enamel surfaces via microwear).

This evidence indicates that more than one tooth type should be evaluated to capture the most accurate palaeoenvironmental signal possible.

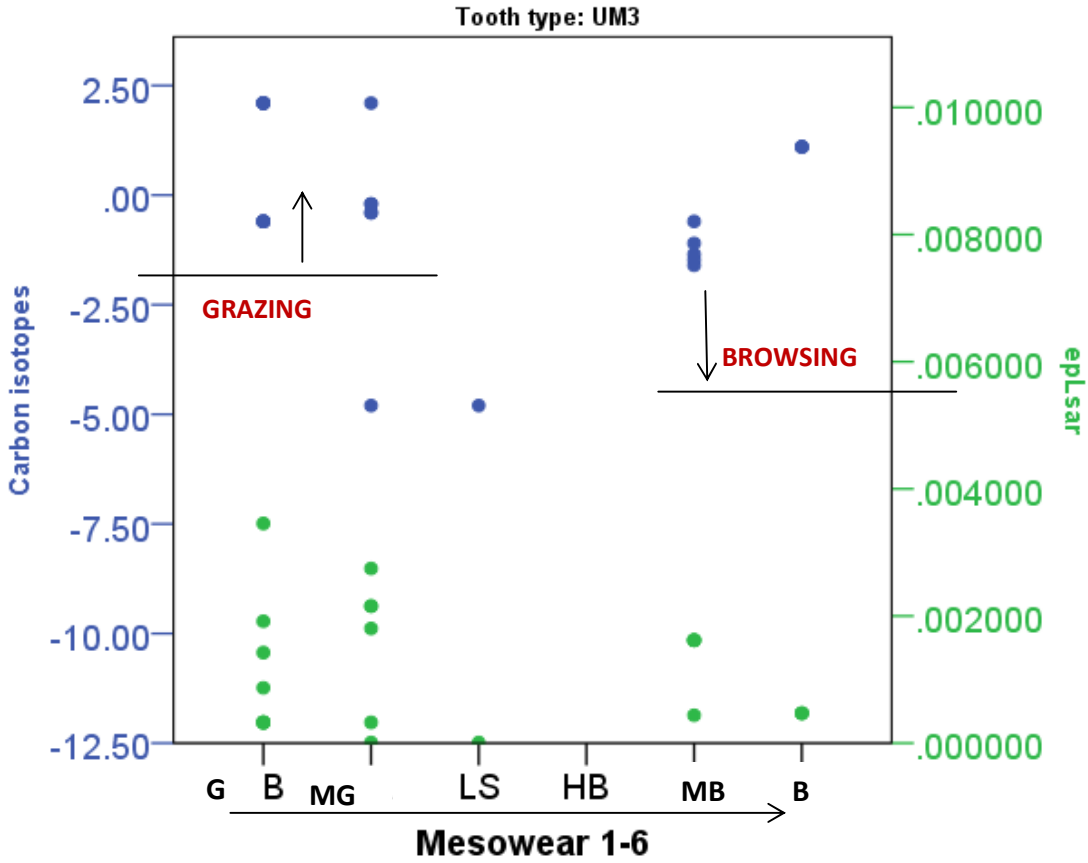


Figure 11.21: Individual Antidorcas from all members M^3 dietary signals from early lifetime (enamel formation) carbon isotopes (left y-axis), last few months of life (anisotropy (epLsar, (in µm)) of enamel facet surface wear) from microwear (right y-axis) and averaged lifetime signal from mesowear (x-axis). Mesowear (x-axis) is displayed from a typical grazing signal on the left (G) on a scale through mixed feeding (MG=mixed/variable grazer; MB=mixed/variable browser) to the right side (B) of grazing to browsing.

Seasonality and Lifetime Dietary Signal

The scale represented by each method informs on slightly differing aspects of the diet. Ackermans et al.'s (2018) mesowear trials on goats found mesowear required at least 6 months to develop to be truly representative of diet. This supports that age of individuals needs to be considered before grouping individuals together for mesowear analysis. Further, seasonal diet is unlikely to differentially manifest as obligate grazing / browsing signals (through cusp shape and occlusal relief) but would presumably display a generalised mixed-feeding signal along with subtle indicators based on the material properties of the vegetation consumed. Microwear and stable isotope dietary signals can inform better on the seasonal discrepancies within deposits.

Table 11.3: Individual Antidorcas comparisons of dietary inferences from all methods, to assess dietary change through individual animal lifetime and attempt to see seasonal change. MDL=mesio-distal length; BLW=bucco-lingual width; CH=crown height; OH=occlusal height; MET=mean enamel thickness. An expanded description is given below the table.

Provenance	**Species**	**Specimen Number**	**Tooth**	**Measurements (mm)**					**Diet**			**Aridity**
				MDL	**BLW**	**CH**	**OH**	**MET**	**Mesowear**	**Microwear**	**$\delta^{13}C$**	**$\delta^{18}O$**
SK M4	*A.cf.recki*	STS1435	RM^2	13.9	10.7	x	1.0	0.73	Variable grazer	x	Browser	wet
	A.recki	STS2369	Rm_3	23.1	8.1	x	2.1	0.80	Mixed	x	Browser	moderate
	A.recki	STS1944	Lm_2	13. 1	7.2	7.3	1.6	0.70	Variable browser	x	Browser	wet
	A.recki	STS1325A	RM^3	16.6	11.9	x	1.0	0.75	Grazer*	x	Browser	wet
	A.bondi	STS1125	Lm_2	12.3	7.0	8.5	2.1	0.90	Grazer	x	Grazer	moderate
SK M5E	*sp.*	S94-6124	M^2	14.5	11.4	x	1.7	0.85	Variable grazer	x	Variable browser	moderate
	sp.	BP/3/16974	M^2	14.8	11.2	x	1.3	0.83	Variable grazer	x	Variable browser	wet
SK M5W	*A.bondi*	S94-7314	Lm_2	12.2	7.9	7.3	0.4	1.07	Grazer	x	Grazer	dry
	sp.	S94-7958	LM^2	15.3	12.5	x	0.7	1.05	Grazer	x	Mixed	moderate
SKX M1	*A.cf recki*	SKX10697	LM^1	12.7	13.6	x	0.3	0.65	Grazer	x	Mixed	wet
	A.recki	SKX4842	M_1	x	6.5	9.1	1.6	0.80	Variable grazer	x	Mixed	moderate
	A.bondi	SKX12067	RM^1	14.9	12.2	x	2.7	1.08	Variable browser	Variable grazer	Grazer	x
	A.bondi	SKX11602	Lm_1	9.8	5.8	19.1	1.6	0.65	Mixed	x	Mixed**	wet-moderate**
	A.marsupialis	SKX10703	RM^3	10.2	9.2	15.3	1.5	0.83	Mixed	x	Mixed	dry
SKX M2	*A.recki*	SK11073	RM^2	x	x	x	x	x	Browser	Browser	Browser	wet
	A.bondi	SK5882	RM^3	13.7	8.9	12.5	2.1	x	Variable grazer	x	Grazer	wet-moderate
	A.bondi	SK4064	RM^3	12.9	6.9	17.0	4.5	x	Mixed	Browser	Grazer	moderate
	A.bondi	SK4083	RM^2	13.9	9.0	15.0	2.9	x	Grazer	Browser	Grazer	dry

	A.bondi	SK4080	RM^2	14.7	10.0	13.8	2.5	x	Mixed	Mixed	Grazer	moderate
	A.bondi	SK2292	LM^3	14.6	8.9	9.8	2.1	x	Mixed	x	Mixed	wet
	A.bondi	SK2366	RM^2	15.3	7.8	10.3	3.6	0.93	Browser	Browser	Mixed	wet
	A.bondi	SK11899	RM^3	15.9	10.1	13.3	2.0	x	Grazer	Variable browser	Grazer	moderate
	sp.	SK5958	Rm_2	15.3	7.8	12.5	2.3	0.57	Variable grazer	Browser	Mixed-variable browser	moderate
	sp.	SK10555	LM^3	15.1	9.2	13.0	2.4	x	Mixed*	Mixed	Grazer	moderate
	sp.	SK6118	RM^3	13.7	8.8	14.2	3.3	x	Browser	Browser	Grazer	moderate
	sp.	SK4633	RM^3	16.1	10.3	12.8	1.9	x	Grazer	Browser	Grazer	wet
	A.marsupialis	SK6106	RM^3	14.7	9.4	12.9	4.6	x	Mixed	Mixed	Grazer	moderate
	A.marsupialis	SK14070	Lm_3	22.3	8.3	11.7	2.2	0.67	Variable browser	x	Browser	wet
	A.marsupialis	SK2953	Rm_3	21.9	7.5	9.7	2.7	0.30	Grazer	x	Browser	wet
	A.marsupialis	SK3055	RM^2	17.2	11.5	9.2	3.3	1.00	Mixed	Browser	Browser	dry
	A.marsupialis	SK5990	LM^3	15.3	8.9	13.3	2.0	x	Mixed	Mixed	Mixed	dry
SKX M3	*A.recki*	SKX35326	LM^1	12.7	11.7	9.7	2.5	0.93	Grazer	x	Browser	moderate
	A.bondi	SKX34249	Lm_3	21.7	7.2	23.4	3.3	0.95	Mixed	x	(seasonal) Mixed**	dry (to moderate seasonally)**
	A.marsupialis	SKX33839	LM^2	16.6	8.6	15.9	2.2	0.80	Browser	x	Mixed-variable browser	moderate
	A.marsupialis	SKX28999	Lm_2	13.95	6.0	8.3	0.5	1.1	Grazer	x	Mixed	dry
	A.marsupialis	SKX28008	LM^2	12.8	11.0	13.1	2.2	1.3	Variable browser	x	Mixed	dry
	A.marsupialis	SKX36545	LM^2	13.2	11.3	15.0	4.3	x	Grazer	x	Mixed	wet

Expanded table information (Table 11.3) Stable isotope data are compiled from published sources (see Isotope chapter for specific references) and data collected for this research by L. Sewell. All other methods were obtained by L. Sewell for this research. Measurements and mean enamel thickness (MET) are included to see the range of variation associated with each species for each time period alongside their dietary indicators. 'sp.' as a species assignment is given where there have been differential identifications by different researchers or if identification was possible only to genus level. Dietary categories are explained fully in each methods' chapter [Mesowear: low relief and blunt-rounded cusps shows an abrasive diet typical of grazing, high relief and sharp cusps suggests a browsing-dominated diet, a combination of these is stated as a variable , e.g. of low relief and sharp cusps is stated as a variable grazer, multiple mesowear variables with conflicting dietary indicators yield a 'mixed' result; microwear: low complexity and high anisotropy suggest grazing-dominance; Stable carbon isotopes: values above -3.0‰ are indicative of C_4 dominance and obligate grazing, below -9‰ are indicative of C_3 dominance and obligate browsing, values between suggest mixed-feeding practices, individuals with $\delta^{13}C$ values close to these boundaries are identified as 'variable' grazer/browser]. $\delta^{18}O$ are taken to be wet if below -1 $\delta^{18}O$ PDB and dry if above +1 $\delta^{18}O$ PDB. Between -1 and 1 $\delta^{18}O$ PDB is classified as 'moderate'. A combination is used if differential signals occur from separate sources.

*'Grazer' or 'mixed' may actually be indicative of an abrasive diet, typically more prevalent amongst grazers. This is true for all 'grazers' identified via mesowear variables as the rounding or blunting of cusps is primarily due to dietary abrasives.

** Serial sampled stable isotopes provide serial results, with categories in this table assigned according to all values.

From the table (Table 11.3) above, *Antidorcas* appear to be individual mixed feeders, varying their diet throughout their lifetime and with individual animal preference within the species. As such, larger sample sizes may be required and in-depth multi-method analyses used to extrapolate palaeovegetation information from their dietary signals. From microwear signals (DMTA), Swartkrans Member 2 shows a relatively strong browsing signal from all *Antidorcas* species present, suggestive of less grassland presence. A more heterogeneous palaeoenvironmental picture emerges however when considering all methods, which may be indicative of *Antidorcas* migratory patterns or herd demographics. Stable carbon isotope values support *A. bondi* being a grazer (Brink & Lee-Thorp 1992). However, *A. bondi* during Swartkrans Member 2 appear to substitute graze in their diet as mixed feeding patterns are evident from lifetime use-wear (mesowear) and end of life (microwear) both for individual animals and intra-specifically; i.e. *A. bondi* from SKX M2 incorporates the dietary spectrum, with some individuals habitually grazing, some habitually browsing and others mixed-feeding.

Antidorcas species life-time dietary signals:

Early life: *A. recki* browsing; *A. bondi* grazing-mixed; *A. marsupialis* mixed (stable carbon isotope values).

Lifetime average: All species are mixed-feeders, individual variations exist through time, within each member for each species (mesowear)

End of life: Mixed-feeding to browsing (DMTA).

The dental enamel of South African browsing herbivores is said to be more enriched in $\delta^{18}O$ than in grazing herbivores. As indicated in the chapter 10, the oxygen isotope composition of the *Antidorcas* dental enamel does not necessarily correlate with the carbon isotope values. In these instances, palaeoenvironmental reasons are deemed greater influential factors than dietary variables. Surprisingly depleted $\delta^{18}O$ values are apparent in

Sterkfontein Member 4 *A. recki* for example. In cooler, wetter environments, there is more standing water. Modern springbok drink opportunistically, so where more is available, they will drink and would therefore have less enriched $\delta^{18}O$ values.

Seasonality of the springbok, along with differential migratory origins (the oxygen content reflecting the local environment during the first year of the springbok's life, whilst carbon allows insight into the diet for the first year) may be achievable from studying the stable isotope values further. This is an avenue for future research.

Individuals Comparisons Review

To extrapolate meaning from each method and understand the timescale it reflects, individual specimens were selected for comparison of all methods (where applicable). Although this yielded small sample sizes, patterns were sought in the data to understand various aspects, particularly, if discrepancies between results from the different methods were due to dynamics such as time averaging of assemblages or lifetime variation of diet within the individual (due to factors such as individual preference, seasonality, migration or ontogeny). Knowledge of these elements, help inform on the palaeoenvironmental context one can infer.

In this instance, observations of potential correlations were hindered by small sample sizes, particularly from the same tooth type, reducing any indication of morphological influence. Differential enamel thickness and isotope correlations across the tooth row highlight how the tooth is used during mastication, with differential exposure to abrasive food particles and pressure exerted on each tooth when chewing. This may also be related to enamel mineralization. Interestingly M1s, which mineralize first, often display the weakest trends. This could be indicative of juveniles feeding differentially to adults within a herd. To rationalize this observation from this starting point, similar studies could be repeated with a larger, exactly comparative dataset.

*Table 11.4: Mean results summaries from each method used for **A. recki** upper second molars, through time. Values are given to 2 decimal places.*

Provenance	**MDL (M^2) (mm)**	**BLW (M^2) (mm)**	**CH (M^2) (mm)**	**ET (M^2) (mm)**	**Asfc (µm)**	**epLsarx10^{-3} (µm)**	**HAsfc (3x3) (µm)**	**MS (1-6) mode**		**Carbon $\delta^{13}C$ (‰)**	**Oxygen $\delta^{18}O$ (‰)**
								upper	lower		
SK M4	13.8	8.2	10.27	0.73	9.22	1.57	0.43	MS	LR	-11.17	26.55
KW	13.5	11.5	x	0.9	2.35	4.60	0.65	LB	LS		
KB											
KE	14.3	8.3	x	0.9	5.06	3.61	0.57	LS	HR		
SK M5								LRS	LR	-10.28	28.52
SK Stw 53											
SK M5E								LR			
SK M5W								LRB	LS		
SKX M1					2.71	3.24	0.81	LB	LS		
SKX M1LB								LR			
SKX M1HR											
KA	13.92	9.56	7.82	0.76	7.21	1.08	0.28	LS	LS		
GD2											
GD1											
SKX M2	12.4	10.1	3.8	0.9				LR	LB	-12.9	x
CC					3.76	3.76	0.98	HS	LS		
SKX M3	12.11	12.0	x	0.87	7.28	1.20	0.40	LR	LB		
PL	13.8	15.0	x	0.73				LS	LSB		
SK LC											
SK PM6											
COH											
GV								LRS			

*Table 11.5: Mean results summaries from each method used for **A. bondi** upper second molars, through time. Values are given to 2 decimal places.*

Provenance	MDL (M^2) (mm)	BLW (M^2) (mm)	CH (M^2) (mm)	ET (M^2) (mm)	Asfc (µm)	epLsarx10^{-3} (µm)	HAsfc (3x3) (µm)	MS (1-6) mode		Carbon $\delta^{13}C$ (‰)	Oxygen $\delta^{18}O$ (‰)
								upper	lower		
SK M4								LR		-1.3	31.17
KW											
KB					2.34	2.35	0.25				
KE											
SK M5	14.46	9.29	8.6	1.0				LR	LR		
SK Stw 53											
SK East								MRS			
SK West								LR	LBS		
SKX M1								HR			
SKX M1LB								LR			
SKX M1HR								LR			
KA	15.3	10.25	8.1	0.97	5.63	5.11	0.39	LRS	LR		
GD2											
GD1											
SKX M2	14.56	9.28	13.8	0.7	5.91	2.26	0.39	MR	LR	-1.09	30.74
CC											
SKX M3	16.0	8.9	x	0.9	1.44	3.39	0.27	MR	HRS		
PL	14.18	9.92	8.0	1.03				LBRS	LS		
SK LC								LB			
SK PM6									LS		
COH	15.25	9.08	9.25	0.7	7.06	3.28	0.88	HS	LR		
GV											

*Table 11.6: Mean results summaries from each method used for fossil **A. marsupialis** upper second molars, through time. Values are given to 2 decimal places.*

Provenance	MDL (M^2) (mm)	BLW (M^2) (mm)	CH (M^2) (mm)	ET (M^2) (mm)	Asfc (µm)	epLsarx10^{-3} (µm)	HAsfc (3x3) (µm)	MS (1-6) mode		Carbon $\delta^{13}C$ (‰)	Oxygen $\delta^{18}O$ (‰)
								upper	lower		
SK M4											
KW	15.73	11.43	x	0.87	2.14	1.22	0.46		HS		
KB											
KE					1.79	2.43	0.54				
SK M5	14.8	13.71	x	1.13				LS	LR		
SK Stw 53											
SK East											
SK West									LBS		
SKX M1	16.3	8.95	12.1	0.73	2.11	3.22	0.66	HR		-8.24	31.71
SKX M1LB								MS			
SKX M1HR											
KA											
GD2					3.70	1.87	0.15		LRS		
GD1											
SKX M2	16.13	10.93	8.45	0.7	3.98	2.53	0.27	LR	LR	-7.82	30.54
CC											
SKX M3	15.84	10.55	14.86	0.8	3.52	3.46	0.47	LR	HRS	-7.27	33.91
PL	13.48	12.13	x	0.97				LS	LR		
SK LC											
SK PM6											
COH	15.02	12.1	10.27	0.97	7.33	2.68	0.45	LS	MS		
GV											

11.4.2 Trends Through Time

Trends through time for *Antidorcas* only are provided in each data chapter (chapters 7-10) for the relevant method. For the following trend through time graphs (Figure 11.22-Figure 11.45), chronology (x axis) runs from c. 2.8 Ma (closest to the graph origin) to Modern (as indicated in Table 2.2), [larger formats with detail of each deposit available on request]. All species used for each method are included on each graph for comparison to the *Antidorcas* data, to better highlight *Antidorcas'* relative diet. Only fossil *Antidorcas*, *Damaliscus pygargus* and *Tragelaphus strepsiceros* are included on any of the graphs within the fossil deposits. All other species only show modern values.

Stable Isotopes

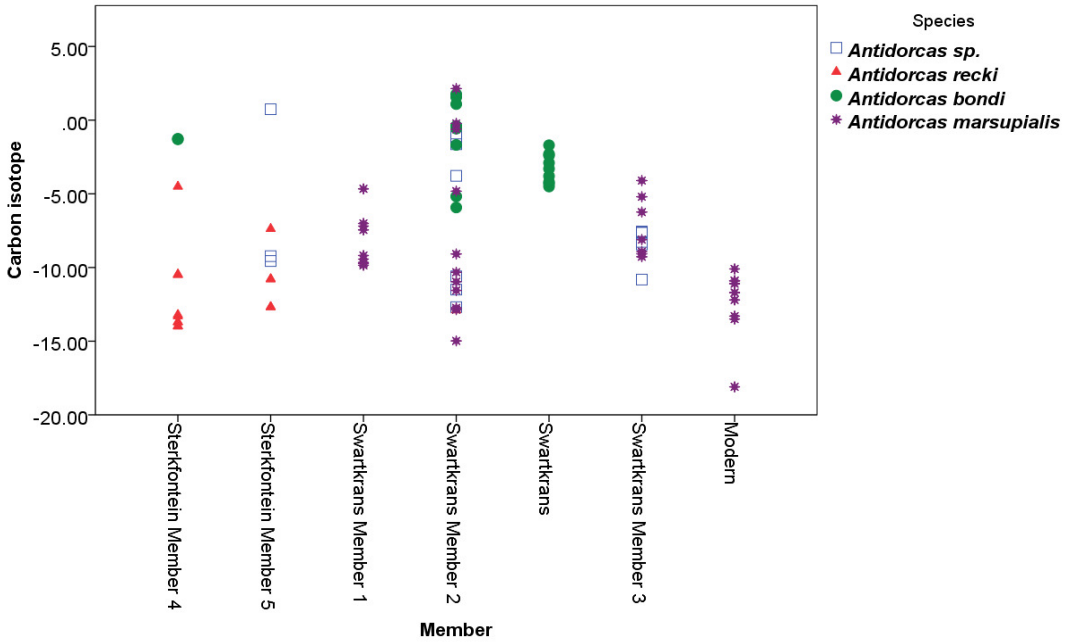


Figure 11.22: Carbon isotope $\delta^{13}C$ values (‰) (Antidorcas dental enamel) through time from 1 Sterkfontein Member 4 (c. 2.8 Ma), through to Swartkrans Member 3 (c. 0.8 Ma) and modern for comparison. Values according to chapter 10 ('Isotopes'). 'Swartkrans' individuals are from published data where this was the only distinction given for provenance.

Chapter 10, Figure 10.6 suggests an increase in aridity through time. The oxygen isotope values $\delta^{18}O$ do not directly correlate with the carbon $\delta^{13}C$ values (Figure 10.4), which would be more indicative of increased browse if they correlated. In Figure 10.4, Figure 10.7 and Figure 11.22 greater dietary variability for *A. bondi* and *A. marsupialis* is shown, ranging across the dietary spectrum from obligate grazing (enrichment in ^{13}C), mixed feeding, to obligate browsing (depleted in ^{13}C). In spite of this, oxygen $\delta^{18}O$ continue to be progressively increasing through time.

DMTA

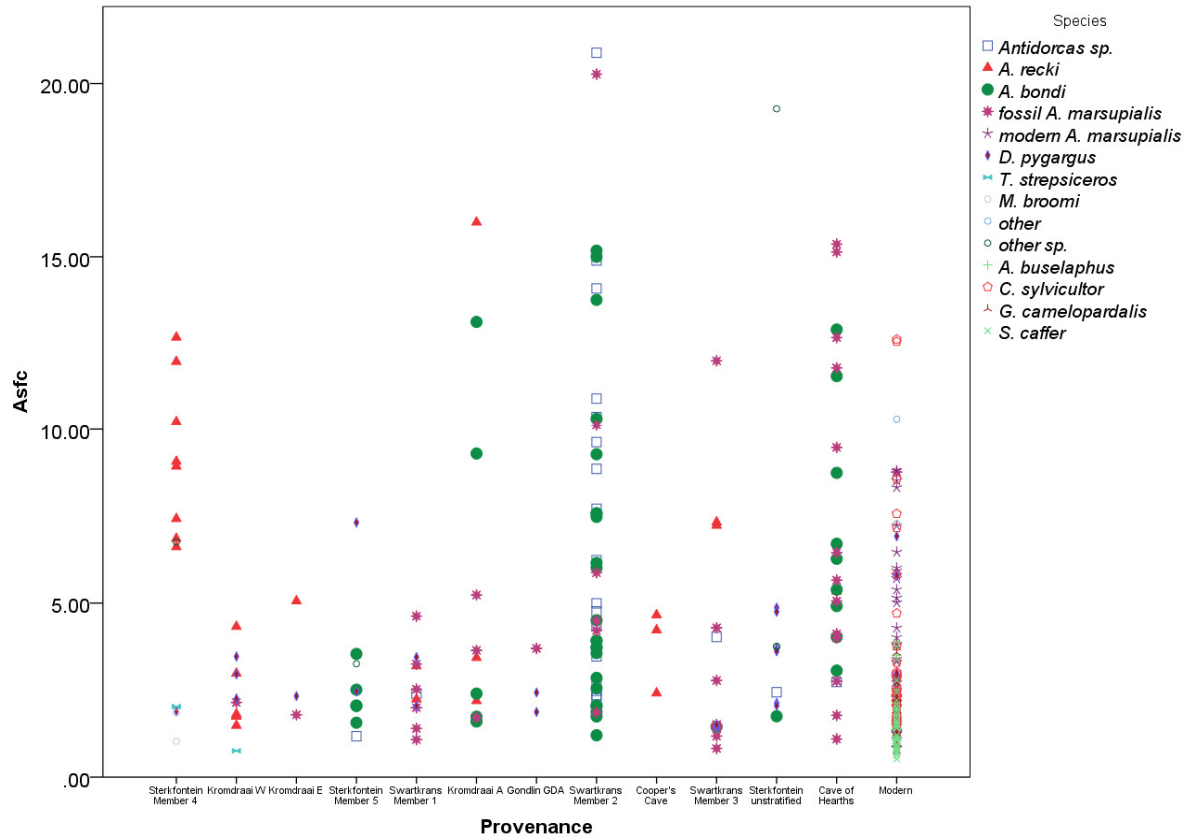


Figure 11.23: Scatter plot showing DMTA complexity (Asfc (in µm)) values through time (arranged in relative chronological order) for all Antidorcas and supplementary species. Higher values are indicative of browsing and closed, woodland-type habitat dominance in the landscape. Data points on the graph have been jittered to more clearly differentiate between individuals.

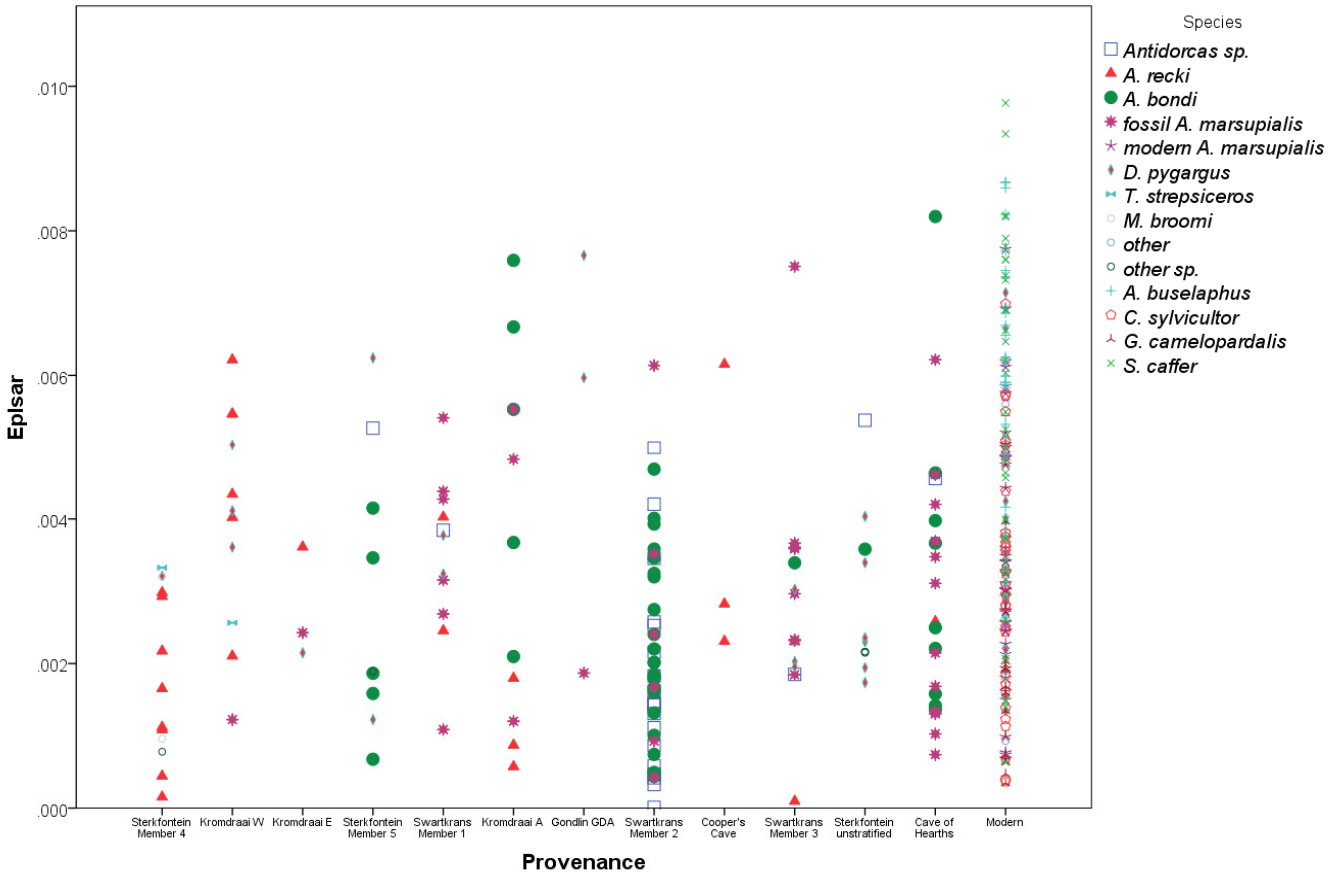


Figure 11.24: Scatter plot showing DMTA anisotropy (epLsar (in µm)) values through time (arranged in relative chronological order) for all Antidorcas and supplementary species. Higher values are indicative of grazing and open, grassland-dominated landscapes. Data points on the graph have been jittered to more clearly differentiate between individuals.

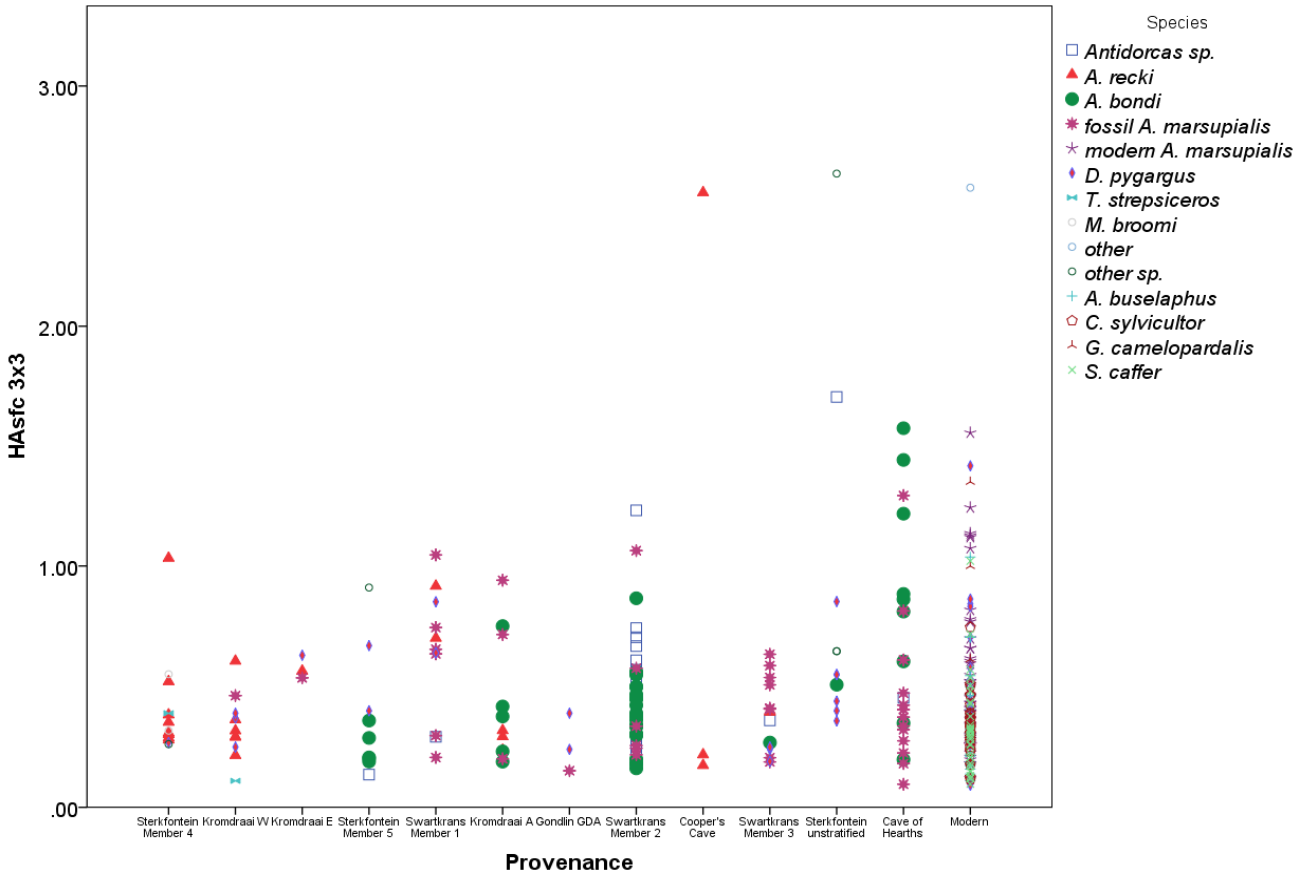


Figure 11.25: Scatter plot showing DMTA heterogeneity (HAsfc ^{9cell} (3x3 scale) (in µm)) values through time (arranged in relative chronological order) for all Antidorcas and supplementary species. Higher values are indicative of mixed-feeding and browsing. Data points on the graph have been jittered to more clearly differentiate between individuals.

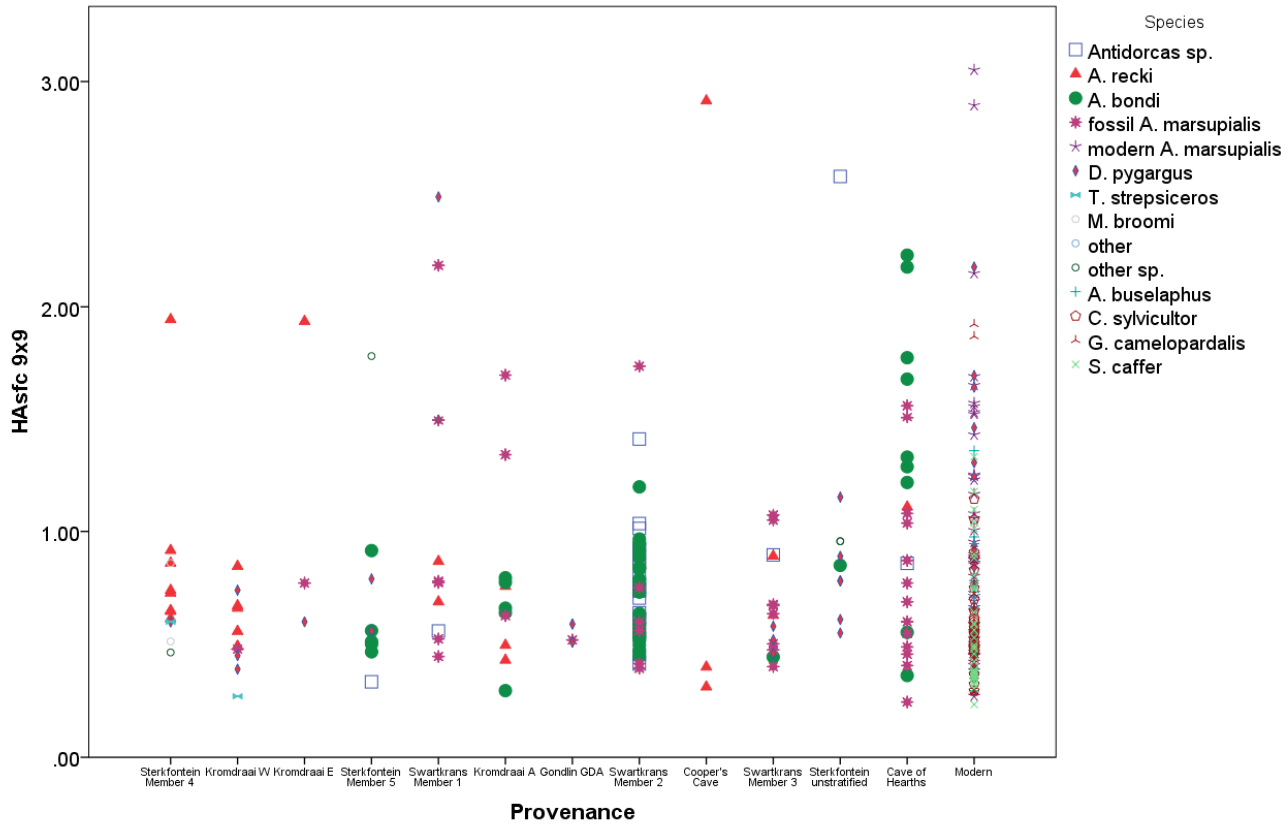


Figure 11.26: Scatterplot showing DMTA heterogeneity (HAsfc 81^{cell} (9x9 scale) (in µm)) values through time (arranged in relative chronological order) for all Antidorcas and supplementary species. Higher values are indicative of mixed-feeding and browsing. Data points on the graph have been jittered to more clearly differentiate between individuals.

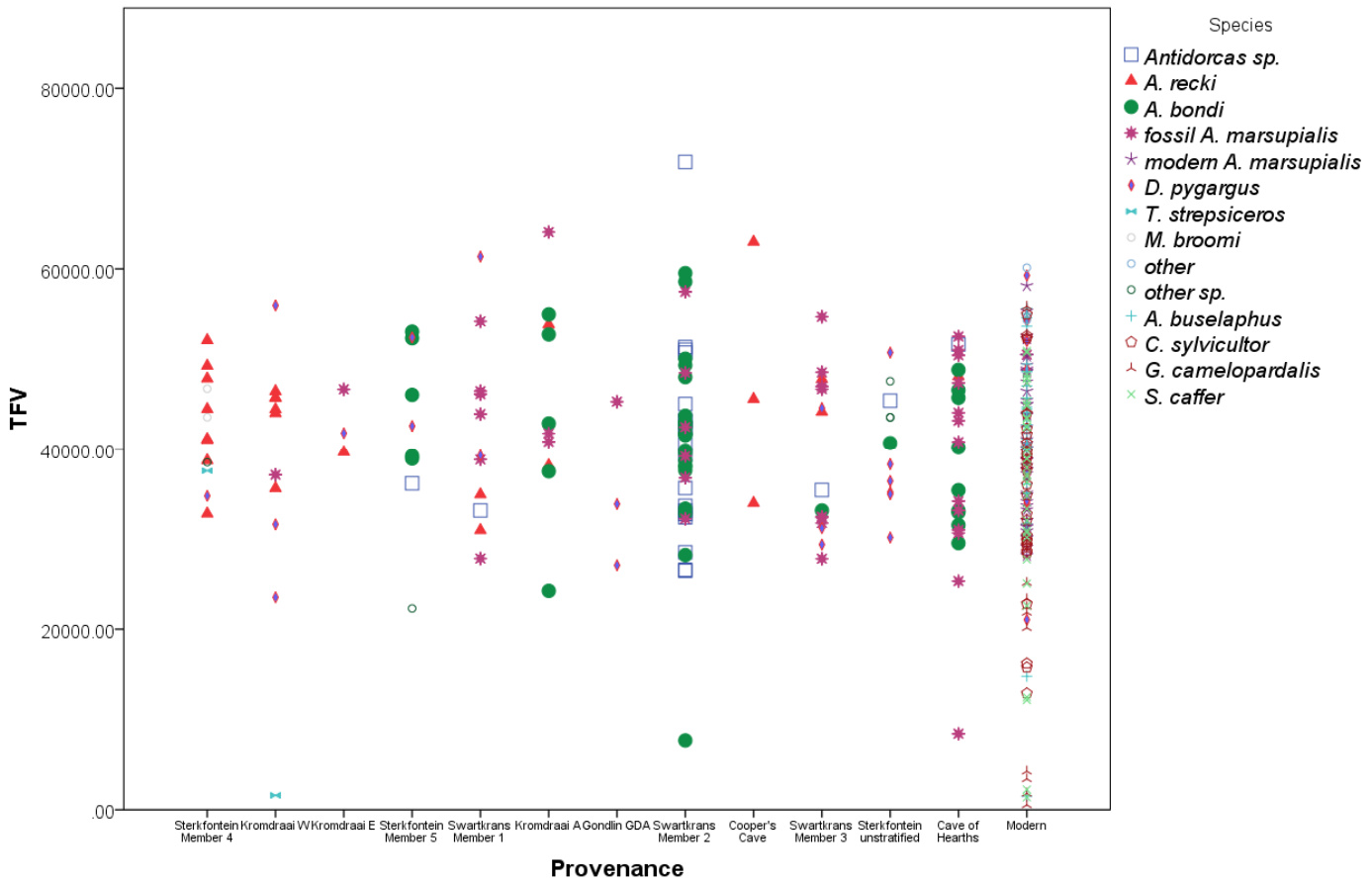


Figure 11.27: Scatterplot showing DMTA textural fill volume (Tfv in (μm)) values through time (arranged in relative chronological order) for all Antidorcas and supplementary species. Higher values are indicative of mixed-feeding and greater habitat heterogeneity. Data points on the graph have been jittered to more clearly differentiate between individuals.

Mesowear

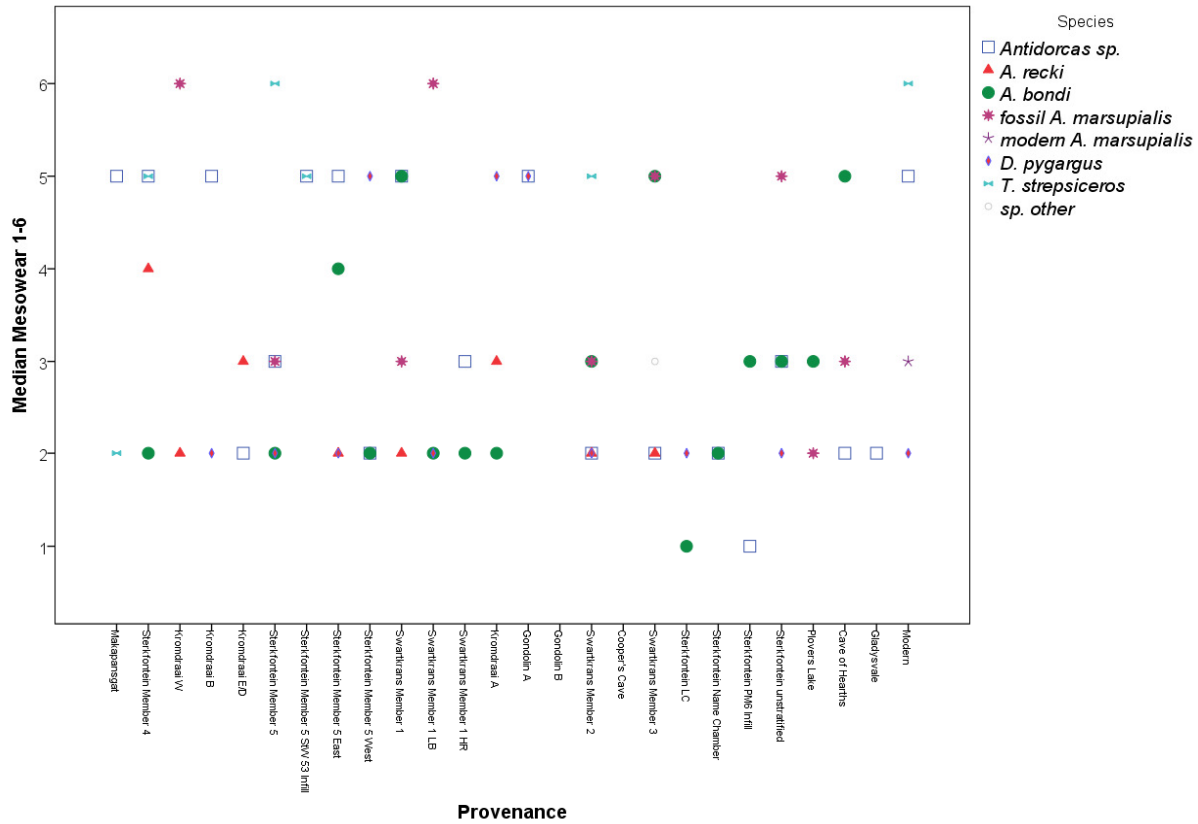


Figure 11.28: Scatterplot showing median Mesowear value for all Antidorcas and supplementary species through time (arranged in relative chronological order). 1=low relief, blunt cusps, 2=low relief, rounded cusps, 3=low relief, sharp cusps, 4=high relief, blunt cusps, 5= high relief, rounded cusps, 6=high relief, sharp cusps.

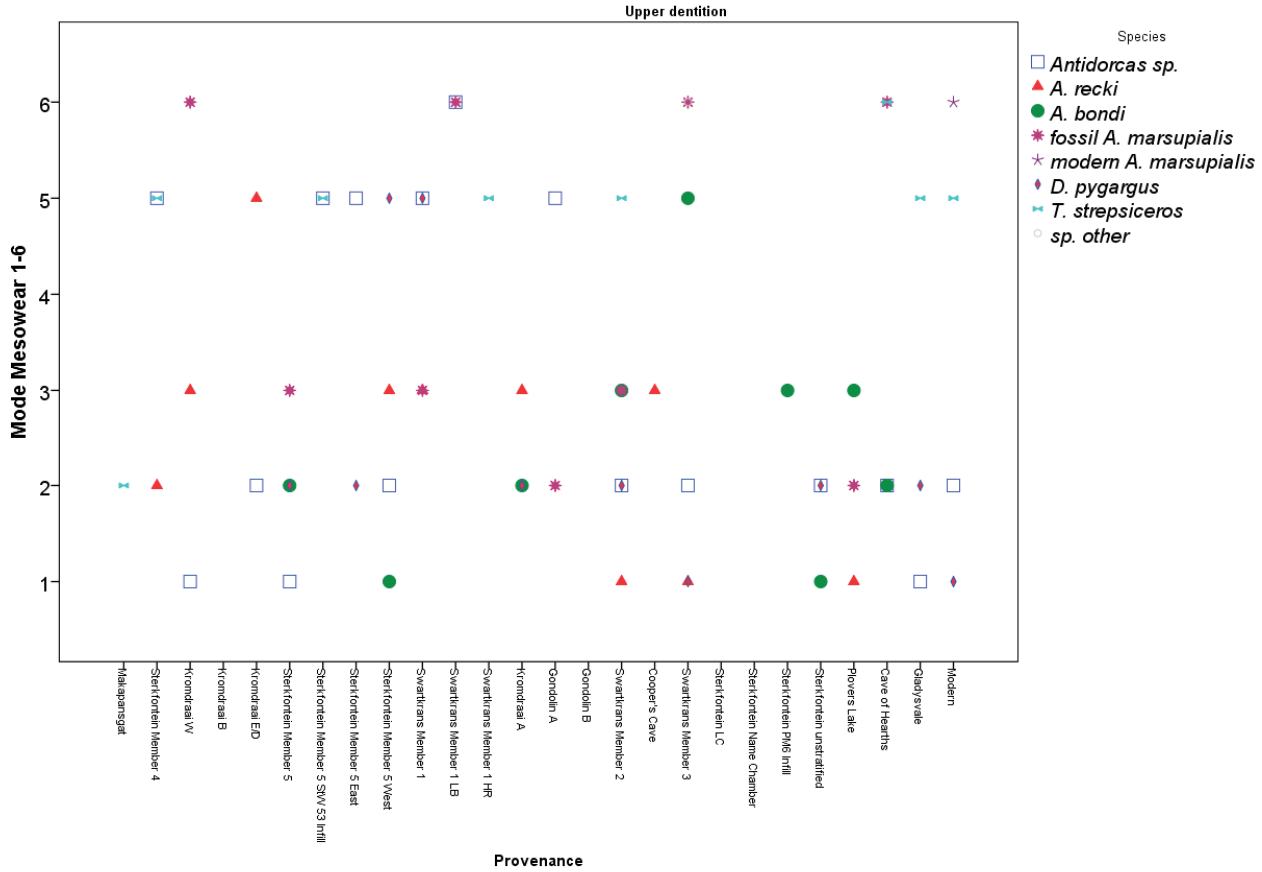


Figure 11.29: Scatterplot showing modal (most frequently occurring) mesowear value for all Antidorcas and supplementary species upper dentition through time (arranged in relative chronological order). 1=low relief, blunt cusps, 2=low relief, rounded cusps, 3=low relief, sharp cusps, 4=high relief, blunt cusps, 5= high relief, rounded cusps, 6=high relief, sharp cusps.

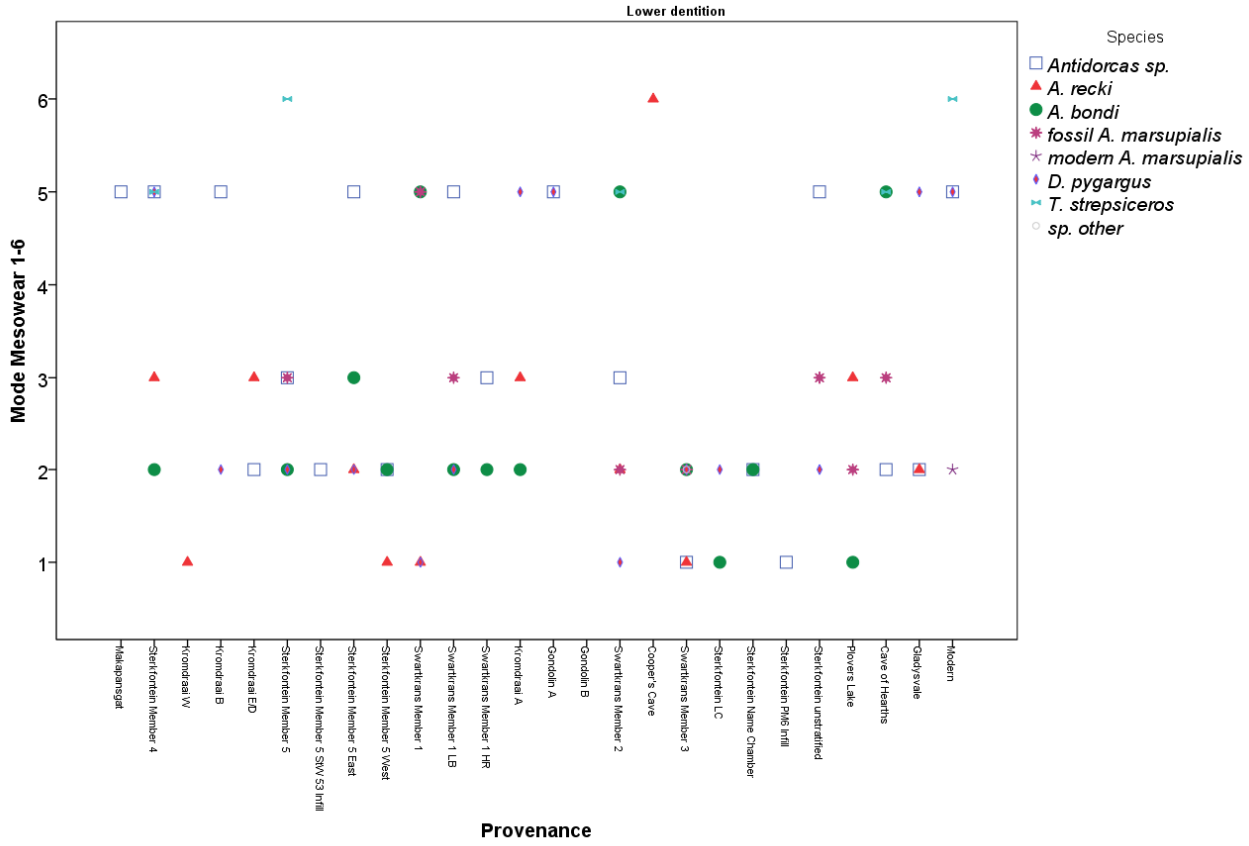


Figure 11.30: Scatterplot showing modal (most frequently occurring) mesowear value for all Antidorcas and supplementary species lower dentition through time (arranged in relative chronological order). 1=low relief, blunt cusps, 2=low relief, rounded cusps, 3=low relief, sharp cusps, 4=high relief, blunt cusps, 5= high relief, rounded cusps, 6=high relief, sharp cusps.

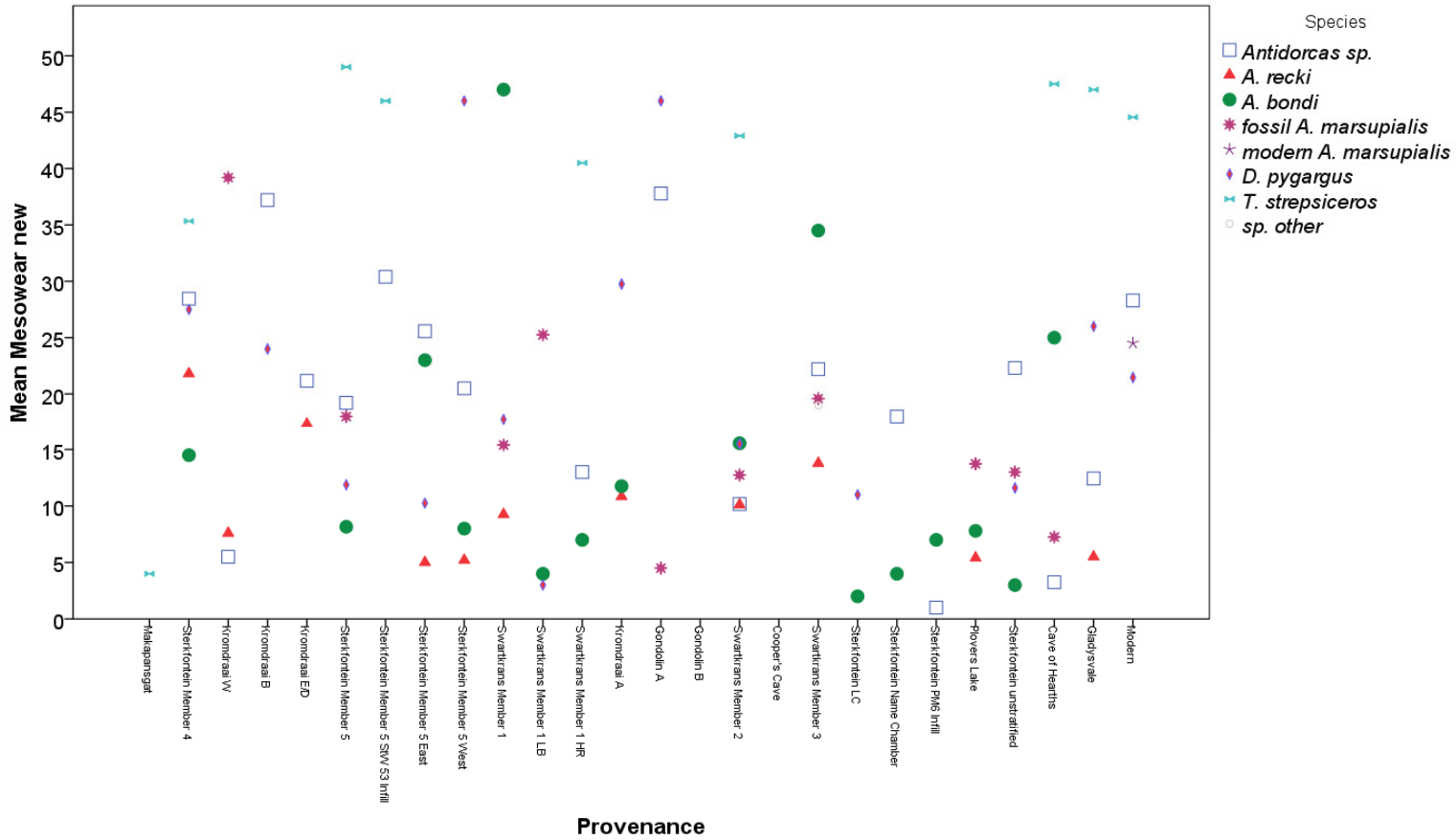


Figure 11.31: Scatterplot showing mean new mesowear score through time (arranged in relative chronological order) for all Antidorcas and supplementary species (new mesowear scores represent a continuous scoring scale 1-49 based on relief and cusp shape, see 'Mesowear' chapter for details; 1 shows low relief, blunt cusps, 49 shows high relief, sharp cusps).

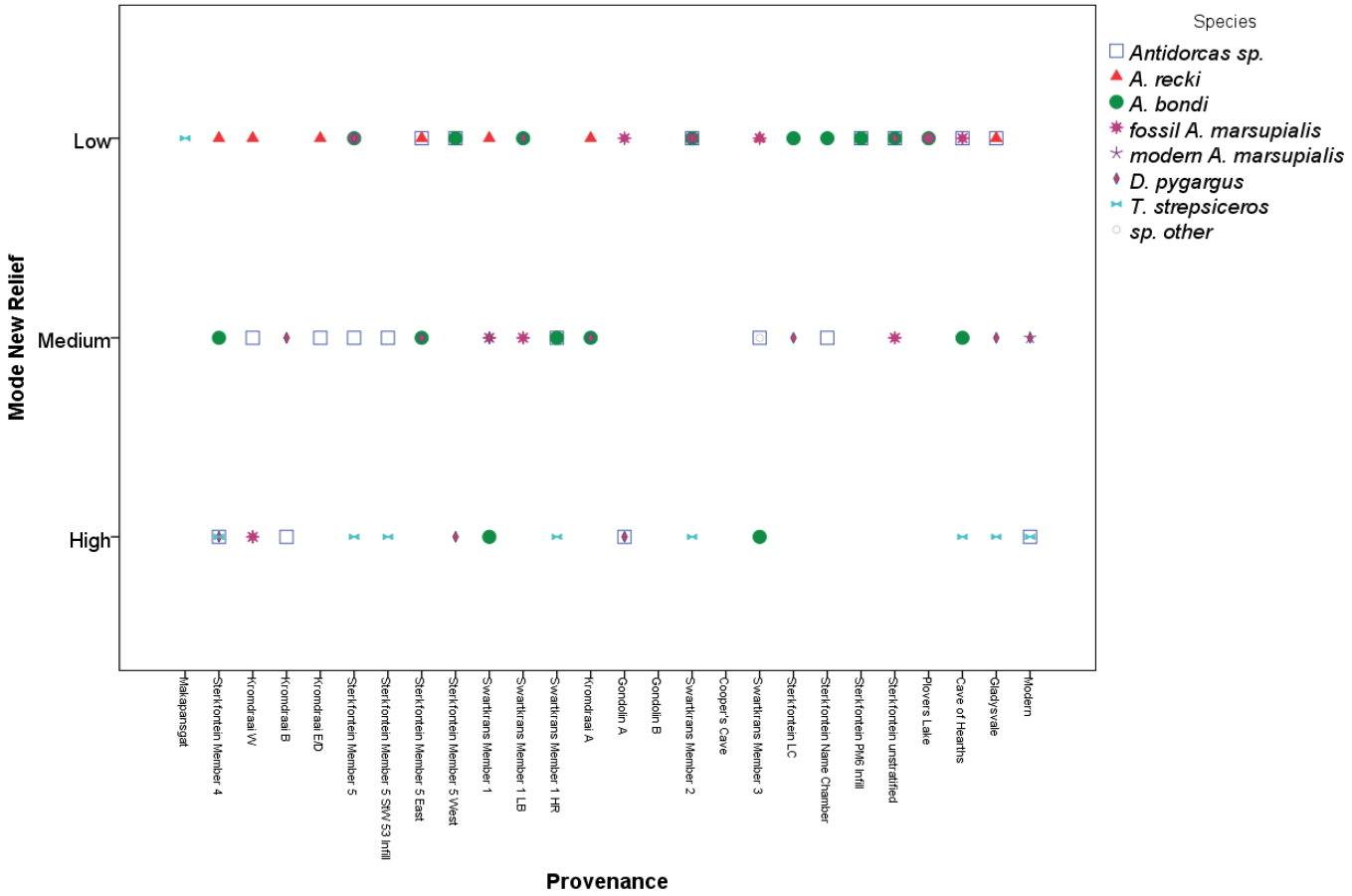


Figure 11.32: Scatterplot shwoing modal (most frequently occurring) mesowear new relief value for all Antidorcas and supplementary species dentition through time (arranged in relative chronological order). 'New' relief includes a 'medium' relief category.

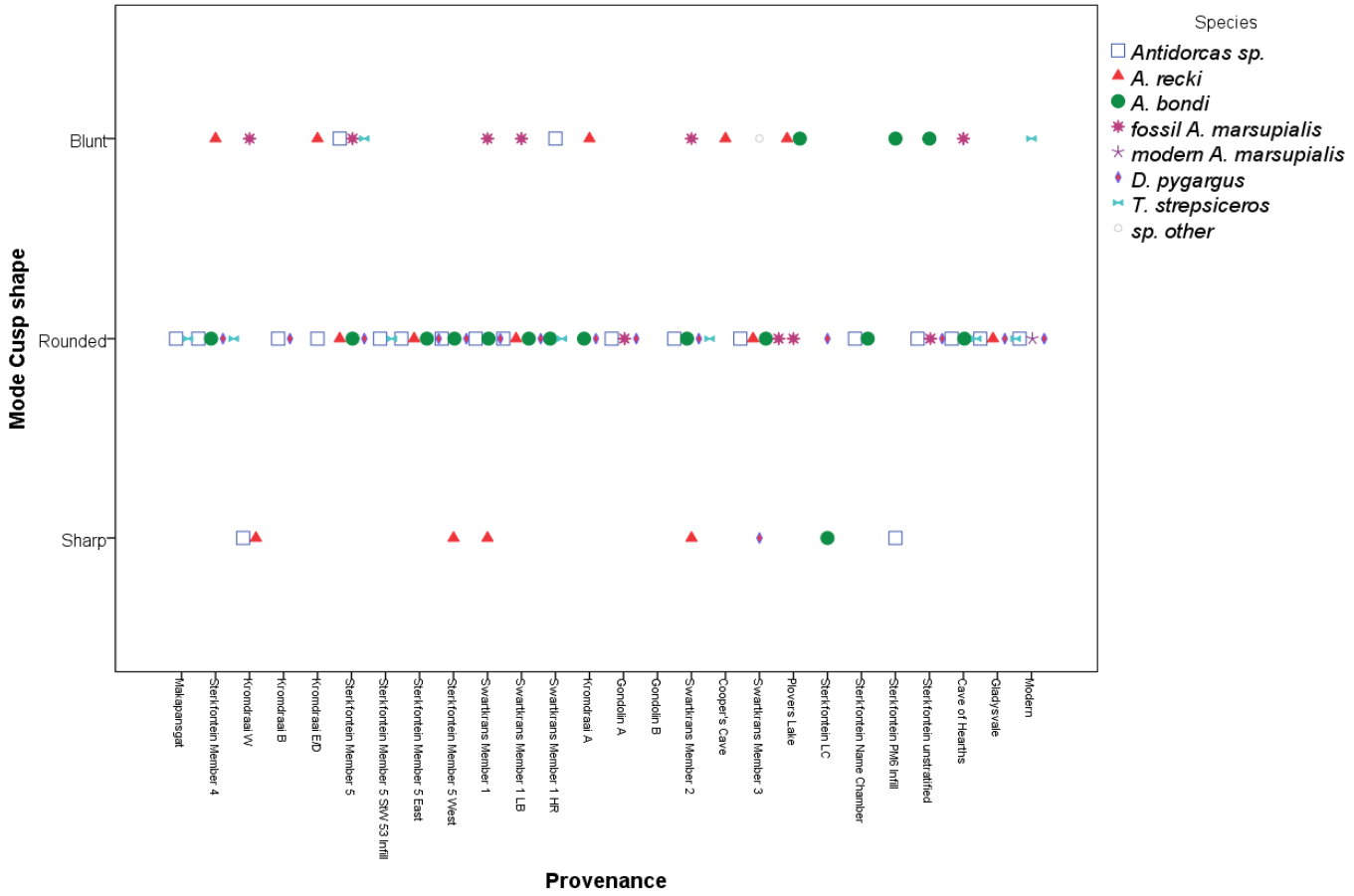


Figure 11.33: Scatterplot showing modal (most frequently occurring) mesowear cusp shape value for all Antidorcas and supplementary species dentition through time (arranged in relative chronological order). Data points on the graph have been jittered to more clearly differentiate between individuals.

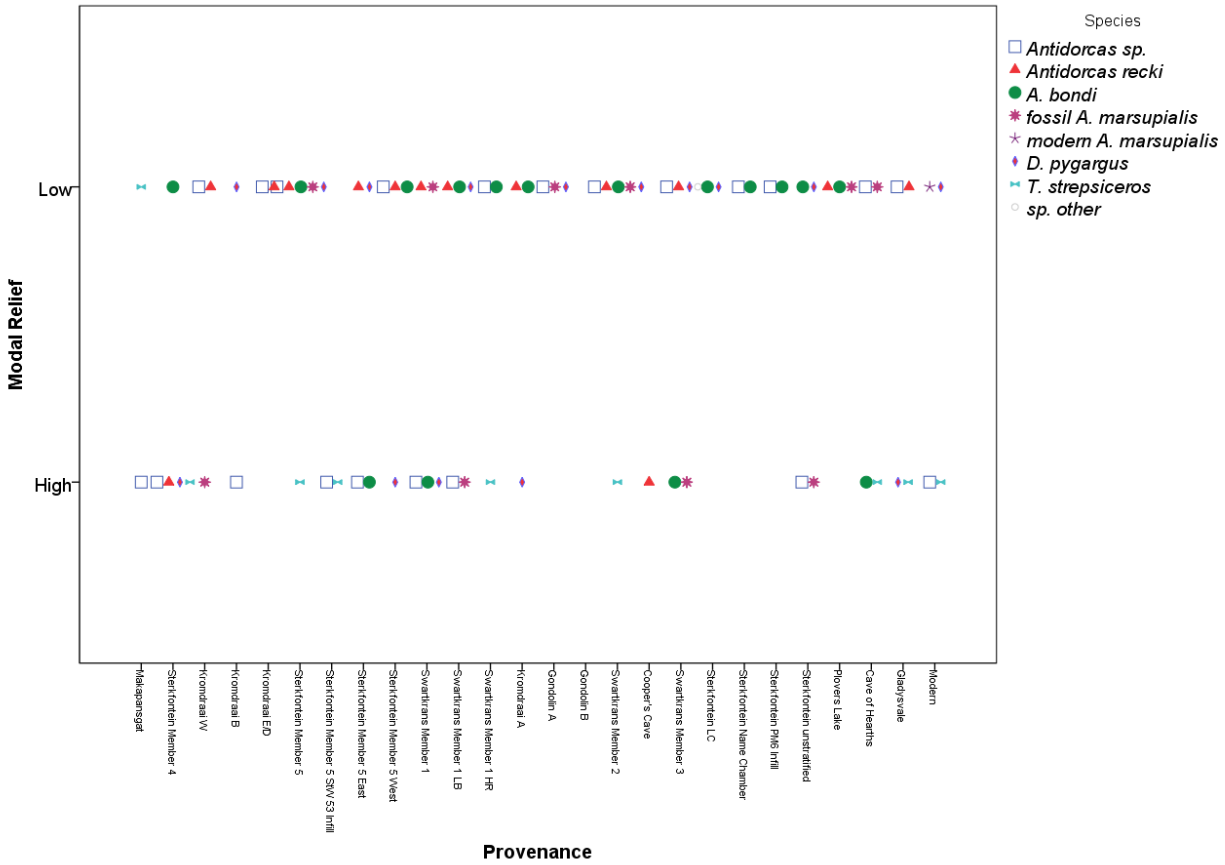


Figure 11.34: Scatterplot showing the modal (most frequently occurring) mesowear relief value for all Antidorcas and supplementary species dentition through time (arranged in relative chronological order). Low relief occurs most frequently. Data points on the graph have been jittered to more clearly differentiate between individuals.

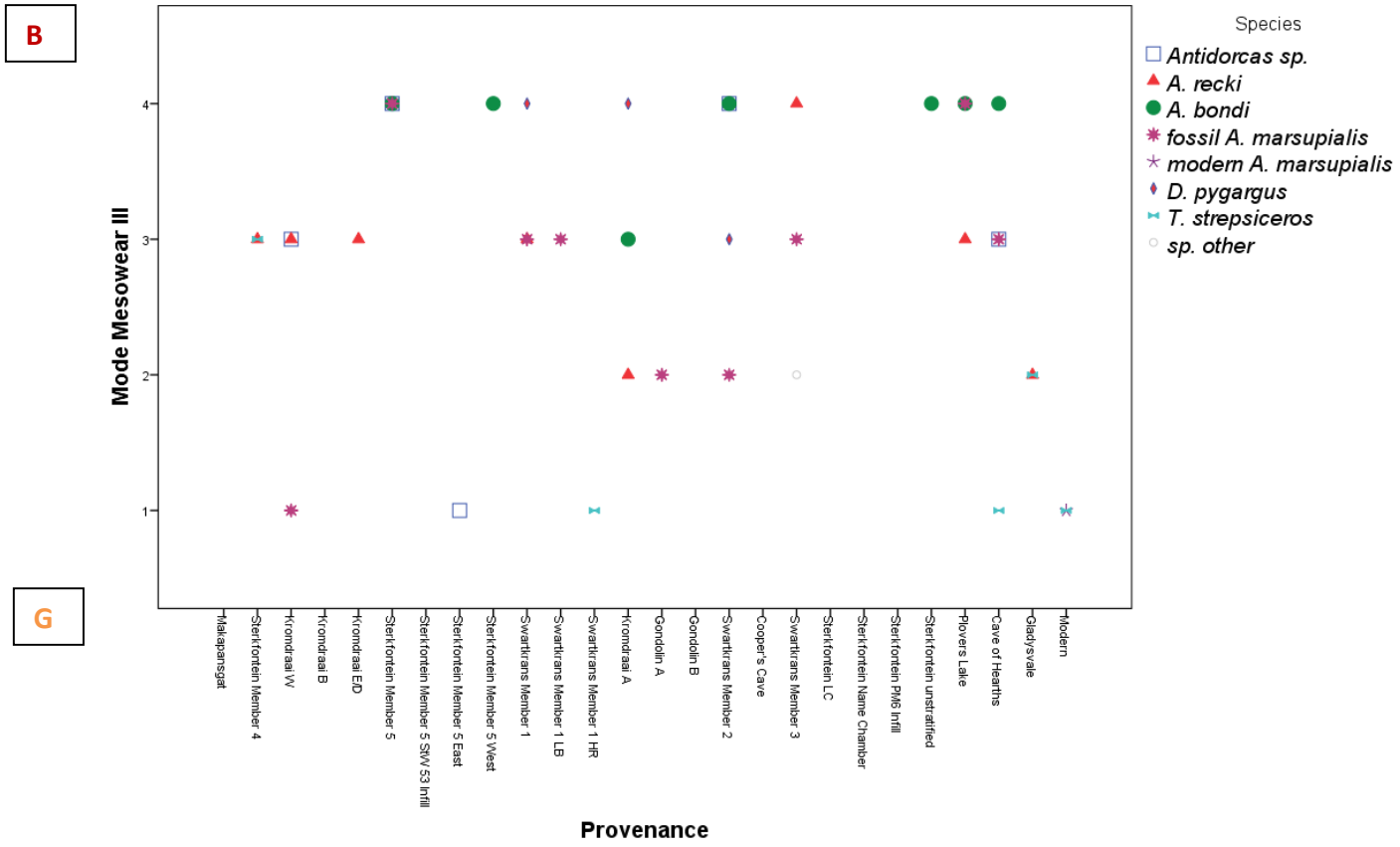


Figure 11. 35: Scatterplot showing modal (most frequently occurring) inner mesowear value (Mesowear III method) for all Antidorcas and supplementary species upper dentition through time (arranged in relative chronological order). 1 is indicative of browsing 'B', through to 4, which is indicative of grazing 'G'.

Dental morphology

Taking the most abundant tooth type in the dataset (maxillary second molar), dental measurements and enamel thickness trends through time are observed.

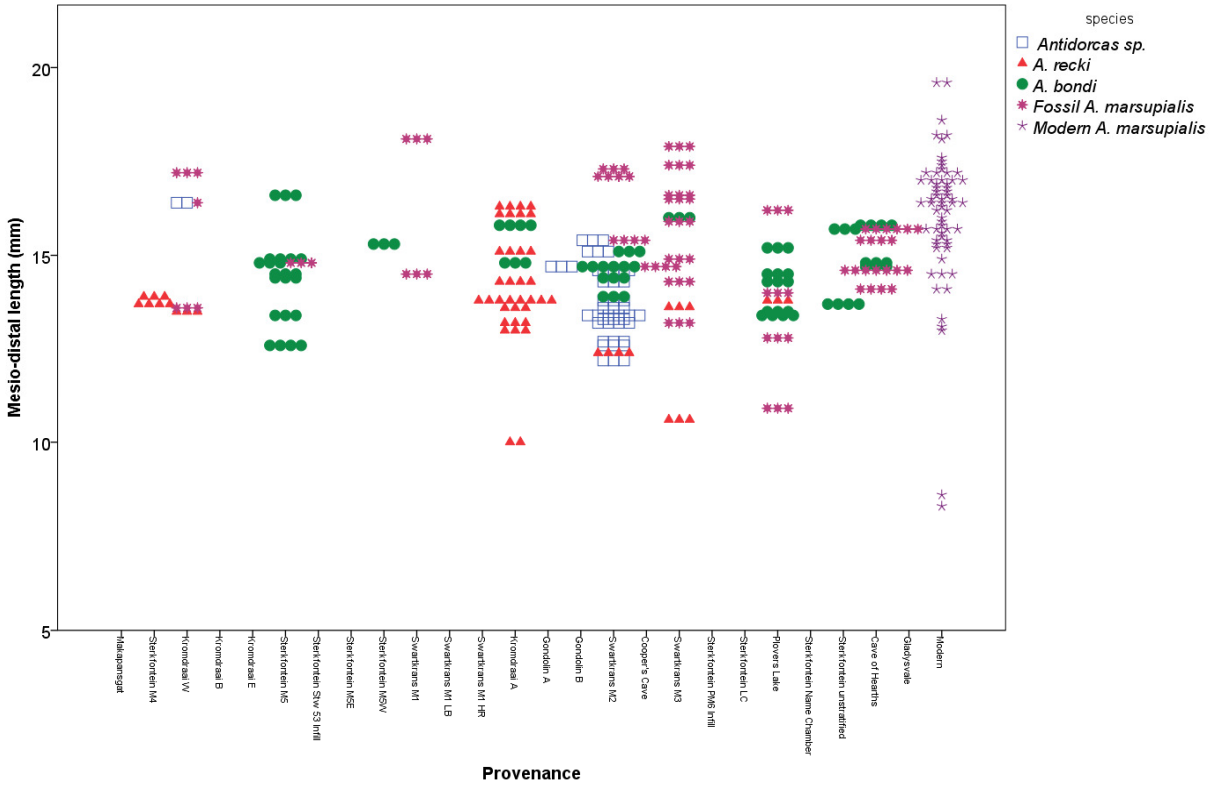


Figure 11.36: Scatterplot of UM2 mesio-distal length (MDL) measurements (in mm) through time (ordered in relative chronology along the x axis from 3.0 Ma to modern) for all Antidorcas species. Data points on the graph have been jittered to more clearly differentiate between individuals.

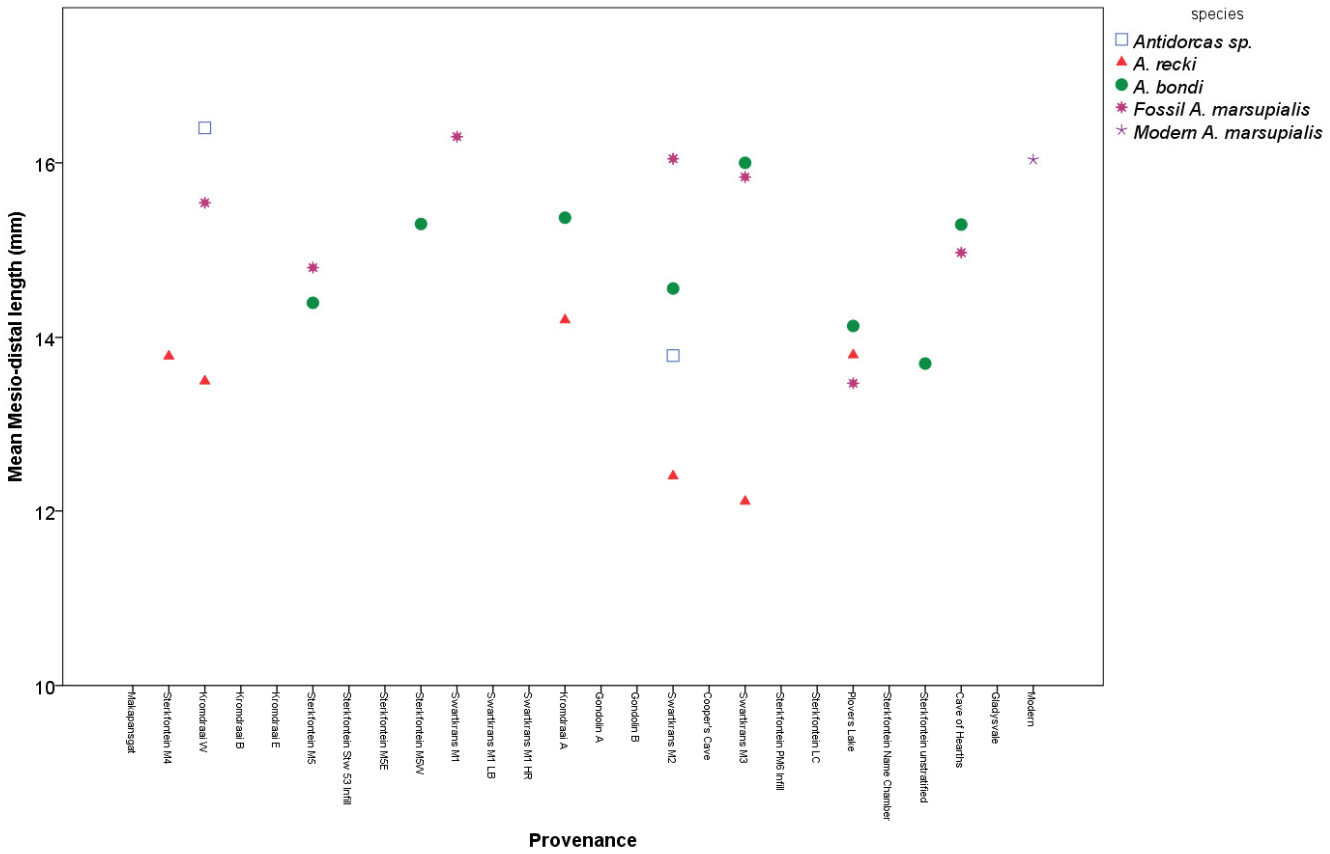


Figure 11.37: Scatterplot of mean UM2 mesio-distal length (MDL) measurements (in mm) through time (ordered in relative chronology along the x axis) for all Antidorcas species.

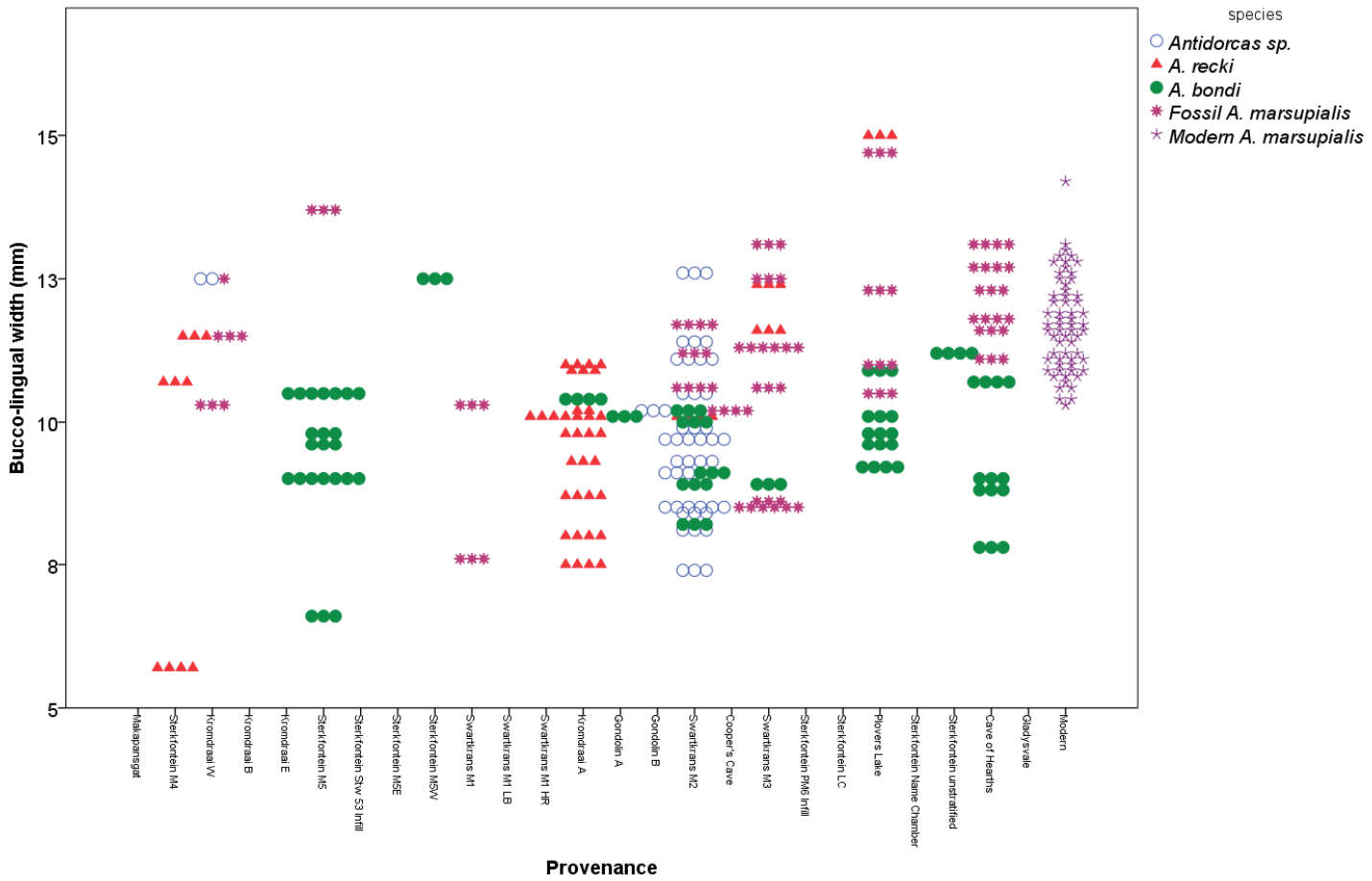


Figure 11.38: Scatterplot of UM2 bucco-lingual (BLW) measurements (in mm) through time (ordered in relative chronology along the x axis) for all Antidorcas species. Data points on the graph have been jittered to more clearly differentiate between individuals.

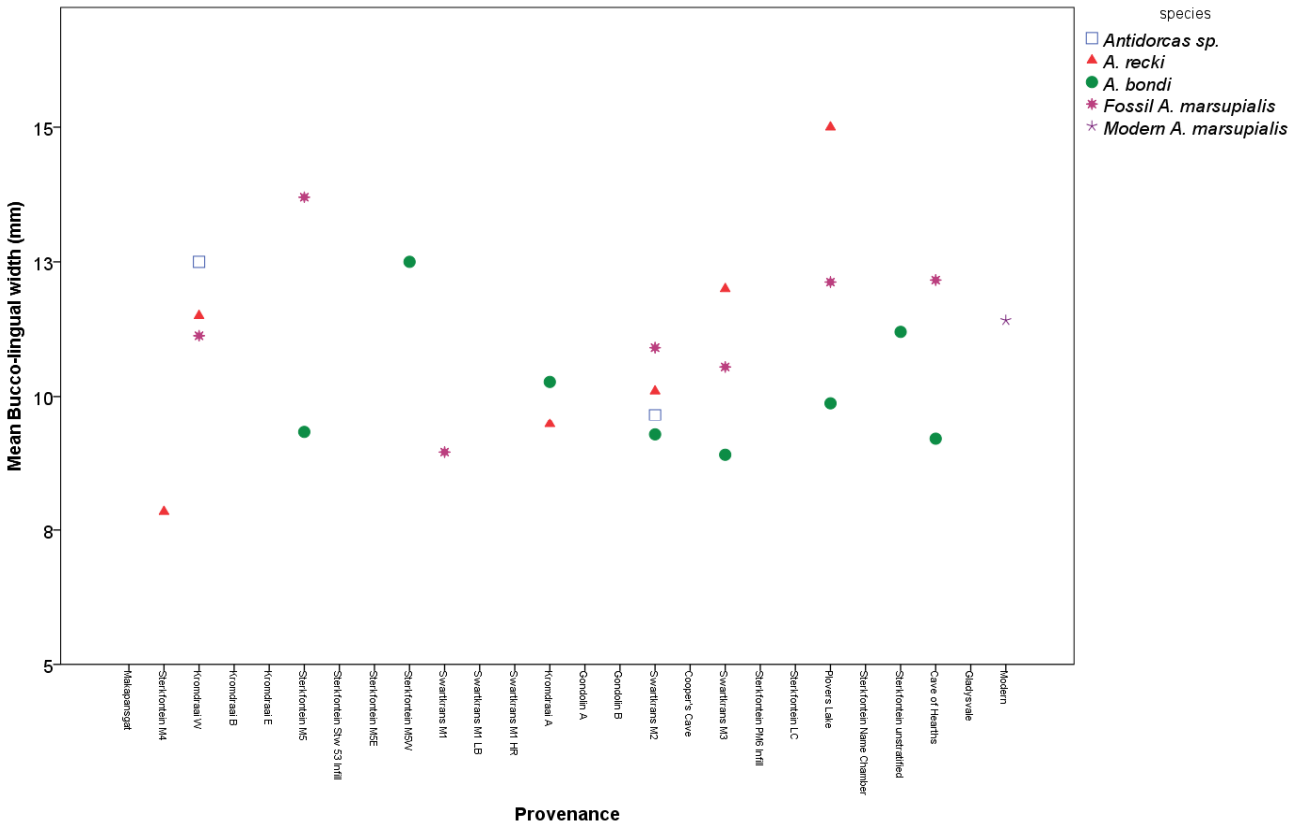


Figure 11.39: Scatterplot of mean UM2 bucco-lingual (BLW) measurements (in mm) through time (ordered in relative chronology along the x axis) for all Antidorcas species.

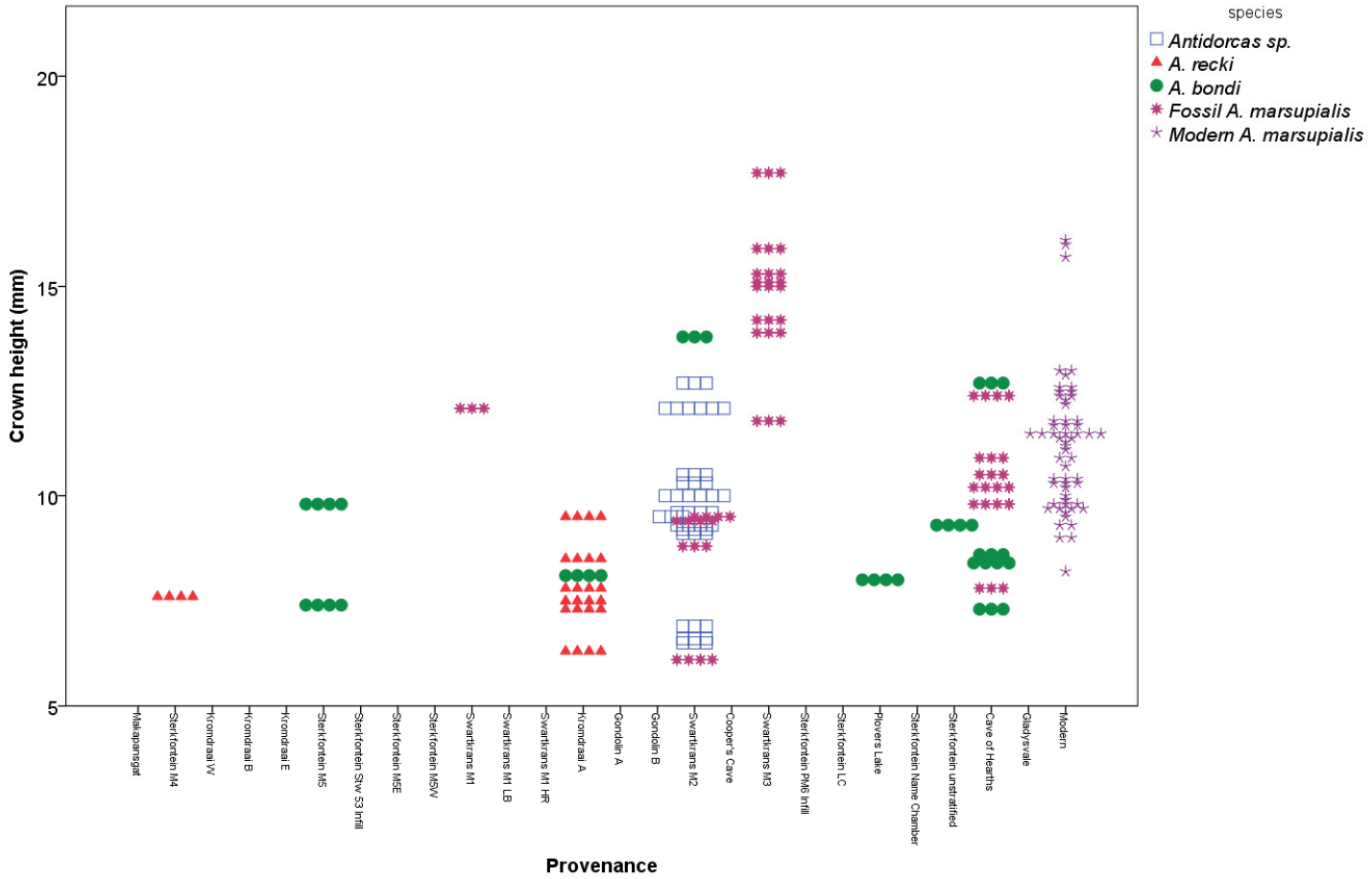


Figure 11.40:: Scatterplot of UM2 crown height (CH) measurements (in mm) through time (ordered in relative chronology along the x axis from Makapansgat c. 3.0 Ma-Modern) for all Antidorcas species. Data points on the graph have been jittered to more clearly differentiate between individuals.

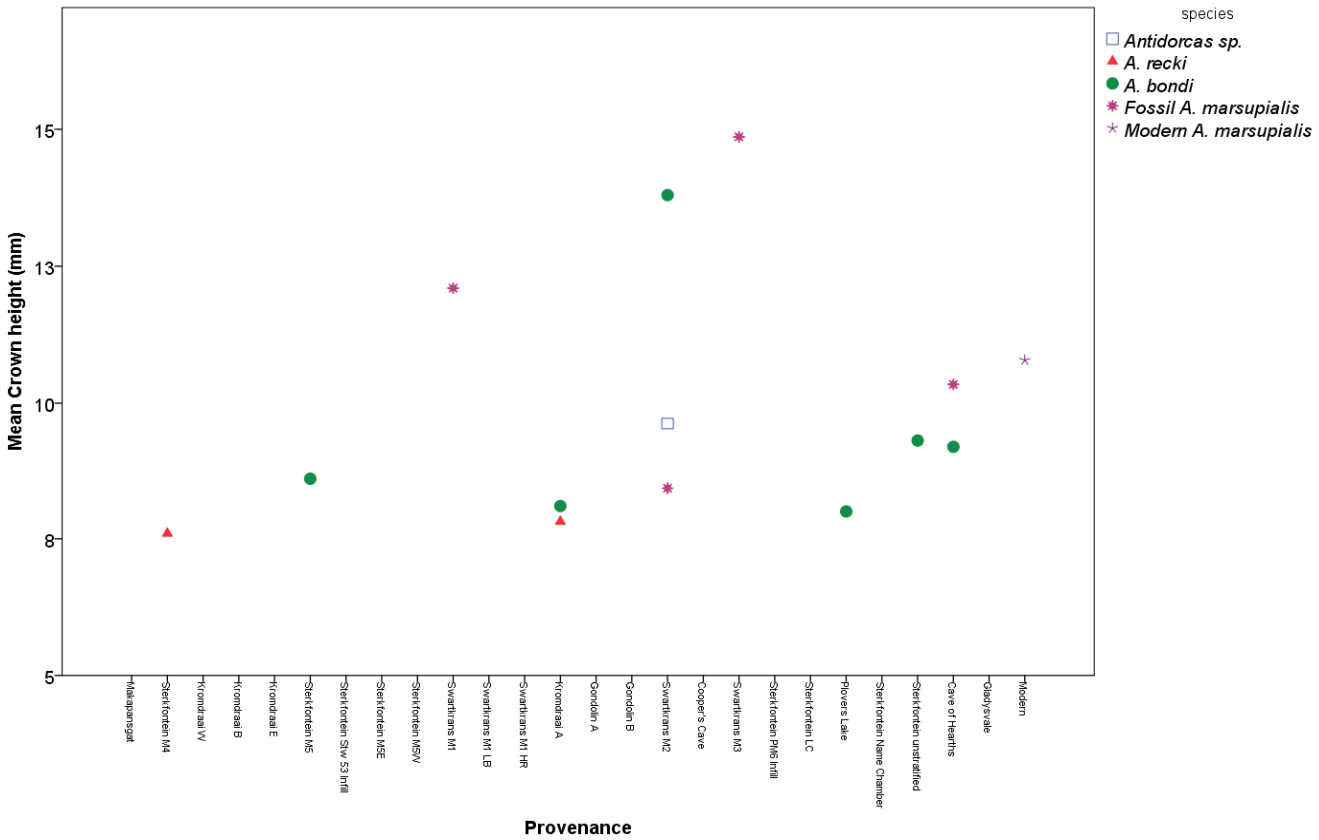


Figure 11.41: Scatterplot of mean UM2 crown height (CH) measurements (in mm) through time (ordered in relative chronology along the x axis) for all Antidorcas species.

Enamel thickness

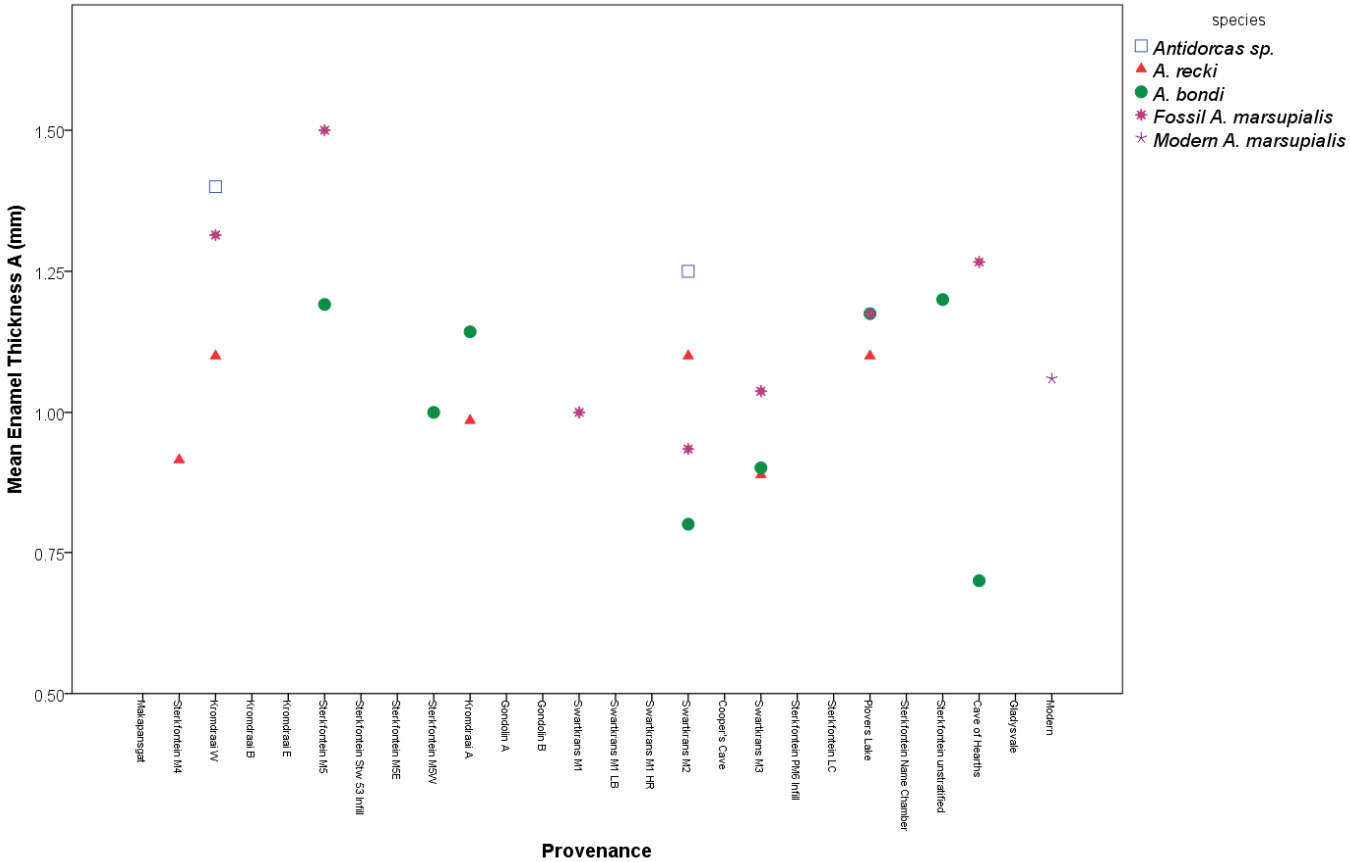


Figure 11.42: Scatterplot of mean upper molar enamel thickness (on lingual enamel facet, location 'A') measurements (in mm) through time (ordered in relative chronology along the x axis) for all Antidorcas species.

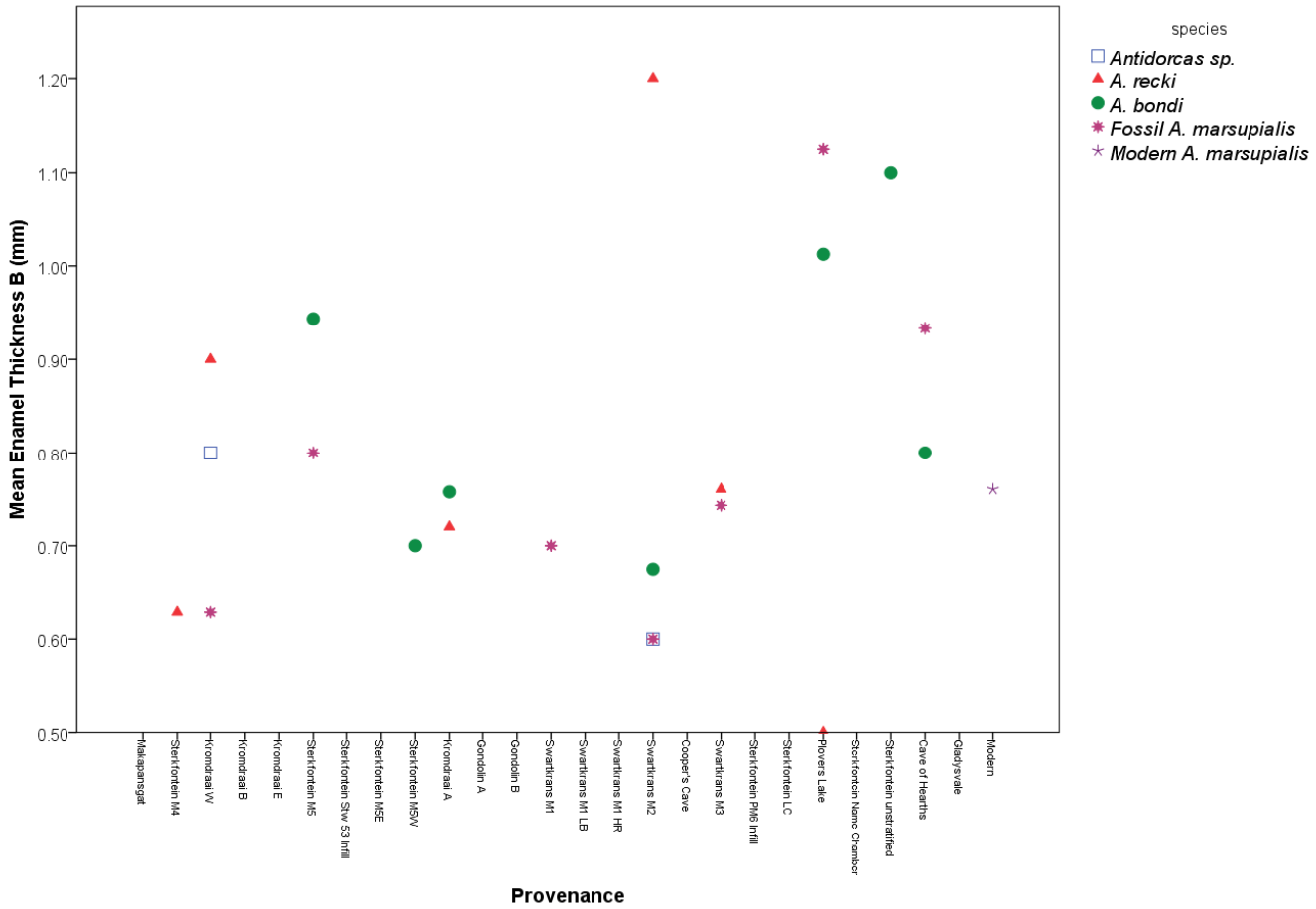


Figure 11.43: Scatterplot of mean upper molar enamel thickness (on inner enamel facet location 'B') measurements (in mm) through time (ordered in relative chronology along the x axis) for all Antidorcas species.

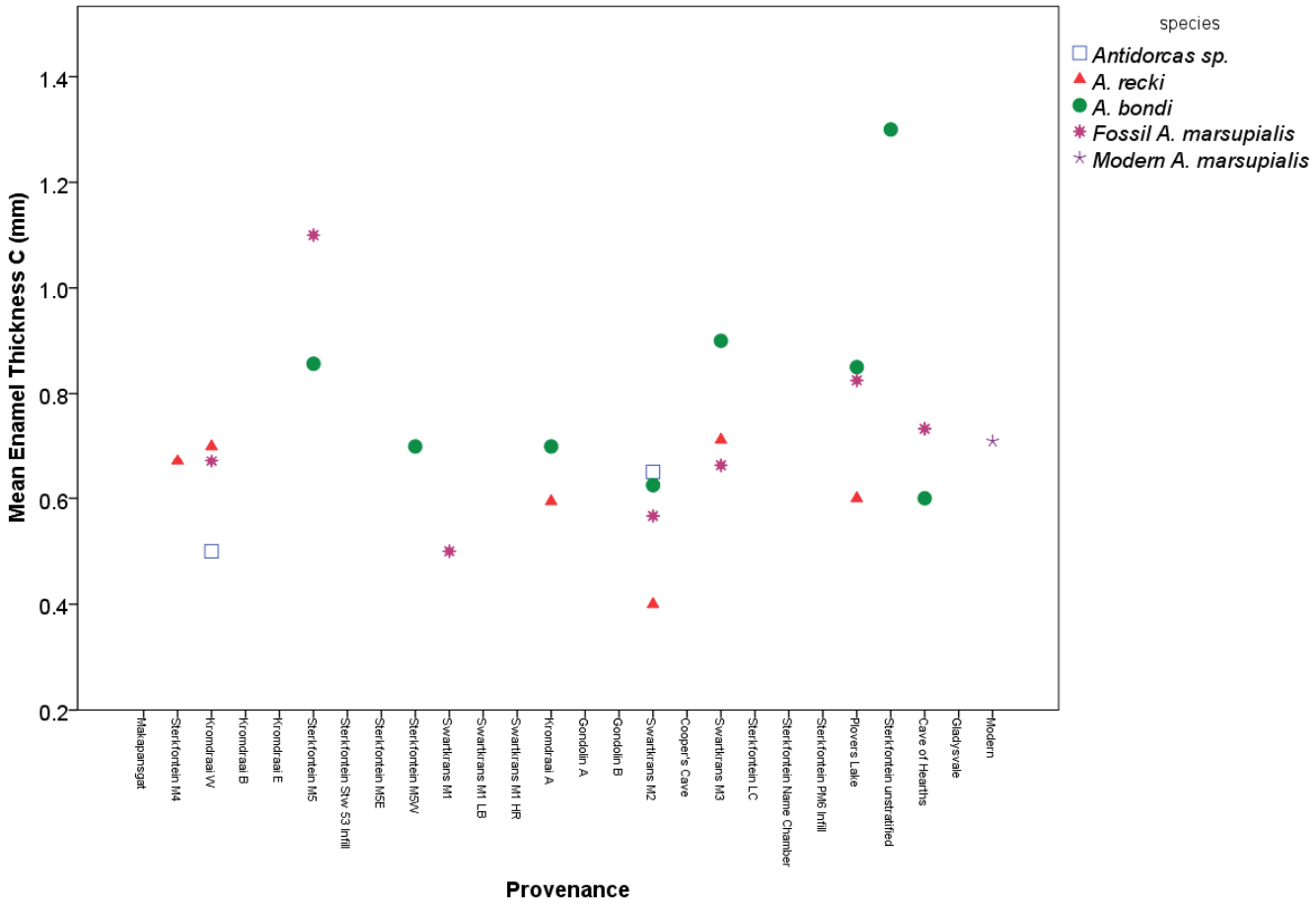


Figure 11.44: Scatterplot of mean upper molar enamel thickness (on buccal enamel facet, location 'C') measurements (in mm) through time (ordered in relative chronology along the x axis) for all Antidorcas species.

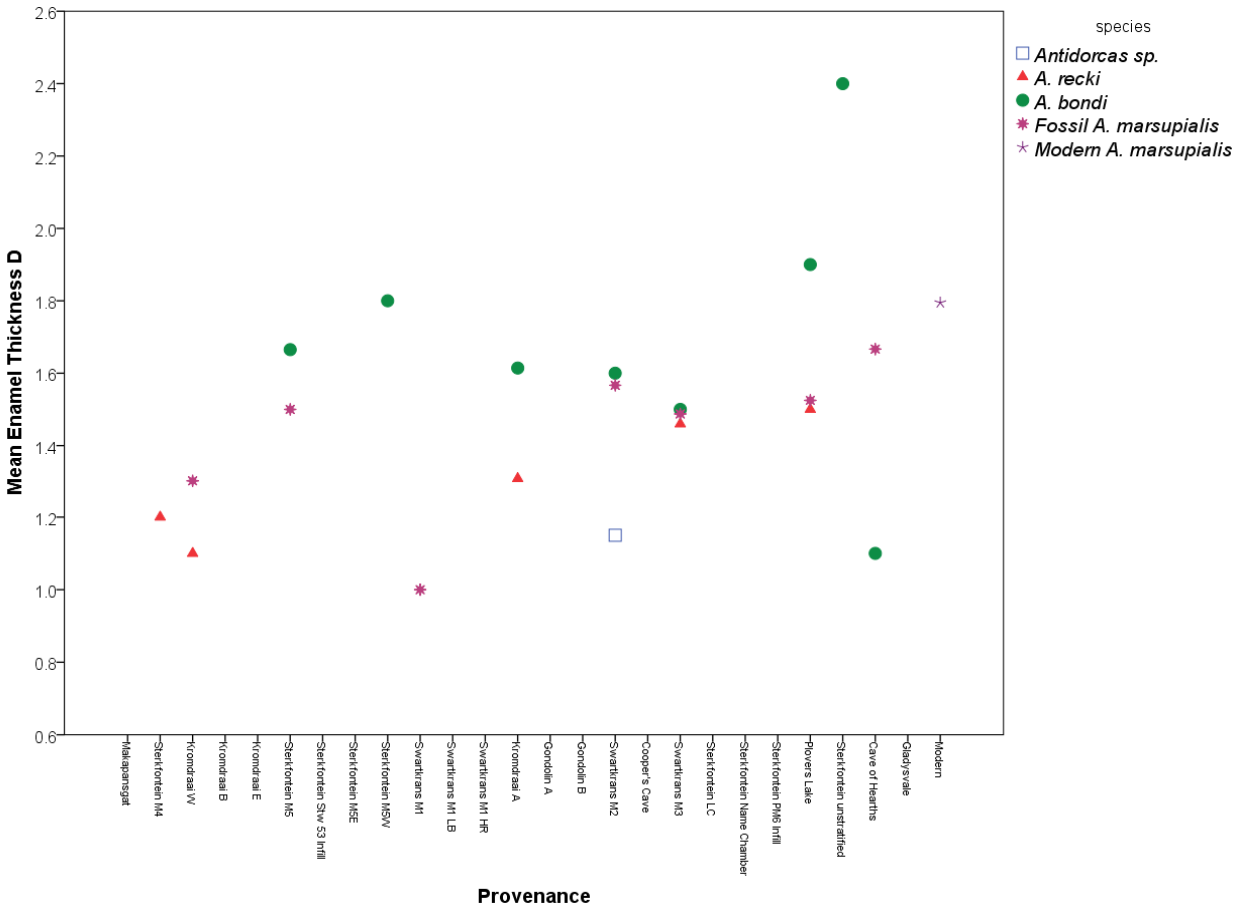


Figure 11.45: Scatterplot of mean upper molar enamel thickness (on mesostyle, location 'D') measurements (in mm) through time (ordered in relative chronology along the x axis) for all Antidorcas species.

Combined Methods Mean results through time

Table 11.7: Antidorcas recki trend through time summary values. Mean measurements are given in mm, mean DMTA values are given in µm, mesowear scores are modal (i.e. occurring most frequently for A. recki in the relevant deposit) and mean isotope values are given in ‰. All values given to 2 decimal places.

	MDL (M^2)	**BLW (M^2)**	**CH (M^2)**	**ET (M^2)**	**Asfc (µm)**	**epLsarx10^{-3} (µm)**	**HAsfc (3x3) (µm)**	**MS (1-6) mode**		**Carbon $\delta^{13}C$ PDB**	**Oxygen $\delta^{18}O$ VSMOW**
								upper	lower		
SK M4	13.8	8.2	10.27	0.73	9.22	1.57	0.43	MS	LR	-11.17	26.55
KW	13.5	11.5	x	0.9	2.35	4.60	0.65	LB	LS		
KB											
KE	14.3	8.3	x	0.9	5.06	3.61	0.57	LS	HR		
SK M5								LRS	LR	-10.28	28.52
SK Stw 53											
SK East								LR			
SK West								LRB	LS		
SKX M1					2.71	3.24	0.81	LB	LS		
SKX M1LB								LR			
SKX M1HR											
KA	13.92	9.56	7.82	0.76	7.21	1.08	0.28	LS	LS		
GD2											
GD1											
SKX M2	12.4	10.1	3.8	0.9				LR	LB		
CC					3.76	3.76	0.98	HS	LS		
SKX M3	12.11	12.0	x	0.87	7.28	1.20	0.40	LR	LB		
PL	13.8	15.0	x	0.73				LS	LSB		
SK LC											
SK PM6											
COH											
GV								LRS			

Table 11.8: Antidorcas bondi trend through time summary values. Mean measurements are given in mm, mean DMTA values are given in µm, mesowear scores are modal (i.e. occurring most frequently for A. bondi in the relevant deposit) and mean isotope values are given in ‰. All values given to 2 decimal places.

	MDL (M^2)	BLW (M^2)	CH (M^2)	ET (M^2)	Asfc (µm)	epLsarx10^{-3} (µm)	HAsfc (3x3) (µm)	MS (1-6) mode		Carbon $\delta^{13}C$	Oxygen $\delta^{18}O$
								upper	lower		
SK M4								LR		-1.3	31.17
KW											
KB					2.34	2.35	0.25				
KE											
SK M5	14.46	9.29	8.6	1.0				LR	LR		
SK Stw 53											
SK East								MRS			
SK West								LR	LBS		
SKX M1								HR			
SKX M1LB								LR			
SKX M1HR								LR			
KA	15.3	10.25	8.1	0.97	5.63	5.11	0.39	LRS	LR		
GD2											
GD1											
SKX M2	14.56	9.28	13.8	0.7	5.91	2.26	0.39	MR	LR	-1.09	30.74
CC											
SKX M3	16.0	8.9	x	0.9	1.44	3.39	0.27	MR	HRS		
PL	14.18	9.92	8.0	1.03				LBRS	LS		
SK LC								LB			
SK PM6									LS		
COH	15.25	9.08	9.25	0.7	7.06	3.28	0.88	HS	LR		
GV											

Table 11.9: Fossil Antidorcas marsupialis trend through time summary values. Mean measurements are given in mm, mean DMTA values are given in µm, mesowear scores are modal (i.e. occurring most frequently for A. marsupialis in the relevant deposit) and mean isotope values are given in ‰. All values given to 2 decimal places.

	MDL (M^2)	BLW (M^2)	CH (M^2)	ET (M^2)	Asfc (µm)	epLsarx10^{-3} (µm)	HAsfc (3x3) (µm)	MS (1-6) mode		Carbon $\delta^{13}C$	Oxygen $\delta^{18}O$
								upper	lower		
SK M4											
KW	15.73	11.43	x	0.87	2.14	1.22	0.46		HS		
KB											
KE					1.79	2.43	0.54				
SK M5	14.8	13.71	x	1.13				LS	LR		
SK Stw 53											
SK East											
SK West									LBS		
SKX M1	16.3	8.95	12.1	0.73	2.11	3.22	0.66	HR		-8.24	31.71
SKX M1LB								MS			
SKX M1HR											
KA											
GD2					3.70	1.87	0.15		LRS		
GD1											
SKX M2	16.13	10.93	8.45	0.7	3.98	2.53	0.27	LR	LR	-7.82	30.54
CC											
SKX M3	15.84	10.55	14.86	0.8	3.52	3.46	0.47	LR	HRS	-7.27	33.91
PL	13.48	12.13	x	0.97				LS	LR		
SK LC											
SK PM6											
COH	15.02	12.1	10.27	0.97	7.33	2.68	0.45	LS	MS		
GV											

11.5 DISCUSSION

11.5.1 Individual Comparisons

Table 11.3: shows dietary variability throughout the life of *Antidorcas* individuals, for all species. More *A. bondi* individuals tend towards grazing and more *A. recki* individuals tend towards browsing, particularly in the earlier Members (e.g. Sterkfontein Member 4) but overall all species have mixed-feeding diets, supporting the range from obligate grazing through mixed to browsing for all *Antidorcas* species. *A. bondi* typically graze in early life and *A. recki* typically browse in early life, no *Antidorcas* species are habitually grazing at the end of life (microwear signals).

A. bondi increasing its browse-consumption through time is a possibility, indicated by increased OH (occlusal height) in Cave of Hearths (c. 0.6-0.4 Ma) (see chapter 7 'Measurements'). This is supported by mandibular mesowear scores, which display higher occlusal relief with no blunt cusps and dominated by rounded to sharp cusps indicative of more browse-dominated diets. This is significantly different from *A. bondi* in Sterkfontein Member 5 (c. 1.8-1.1 Ma), which is dominated by lower relief with blunt and rounded cusps. The suggestion of *A. bondi* increased browse consumption also correlates with the DMTA results for *A. bondi* (see chapter 9).

A.bondi individuals from SKX M2

SK 2366 has carbon isotope values (early life) that are indicative of mixed-feeding. However, mesowear and microwear indicate a more dominant browsing diet. Although displaying hypsodonty, the relatively low crown height (compared to other *A. bondi* individuals) also supports inference of a browsing diet. As hypsodonty is an adaptation by *A. bondi*, being selected for over generations, the reduced hypsodonty is potentially reflective of reduced grazing and selection against hypsodonty [Originally identified by Vrba (1973, 1976) as potentially *A. australis*].

SK 5882 (no microwear) and **SK 10555** are both shown to be grazers from all methods.

The range of variation in *A. bondi* M2 measurements and dietary indications may support the idea of a transitionary period, perhaps during a period of environmental instability with no one direction for selection pressure. However, Maxwell et al. (2018)'s research encourages caution. Swartkrans Member 2 has a much higher abundance of *Antidorcas*, specifically of *A. bondi* compared to the other provenance (including the other members at Swartkrans). The Swartkrans Member 2 assemblage could be reflective of more variability within the living assemblage being captured in the fossil record (i.e. differential preservation) compared to other time periods, rather than increased variability in the living assemblage compared to other time periods. Yet the question remains as to why there is an increased abundance of *Antidorcas* in this Member, this may in itself point to increased instability. The same excavation and post-excavation team were responsible for the entire Swartkrans site so excavation bias is unlikely.

There is the possibility that an increased abundance of *Antidorcas* could still be due to increased preservation. In spite of similarities in genera present (evidenced via the meta-analysis in chapter 5), the members within the site could be subject to differential taphonomic and diagenetic agents.

11.5.2 Species Comparisons

Antidorcas palaeoecology

Stable carbon isotope ($\delta^{13}C$) values support Brink & Lee-Thorp (1992)'s suggestion of *A. bondi* as a grazer. However, this is not supported by use-wear. It is possible that *A. bondi* is made to rely on fall-back vegetation, adopting a browsing diet that they were unable to process in the days before death (microwear) around the Cradle of Humankind sites and may highlight cause of death. However, the mesowear variables also go against catholic grazing for *A. bondi*. Therefore, it seems more likely that *A. bondi* herd demographics saw the young graze (whilst enamel formation occurred and reflected by isotopes) while the adults depend more on browse (as seen through use-wear). Alternatively, the difference could be reflective of seasonality and/or migration. Use-wear shows a dominance of mixed feeding, which could be seasonal and has the potential to be from various locations (along a migration route), culminating in microwear showing browse. Animals are more likely to die when preferred resources are low, which is more likely during winter months. If, as Brink and Lee-Thorp propose, *A. bondi* was the smallest member of a grazing succession, feeding on the new grass shoots before they lignify, a seasonal shortage of grass would make *A. bondi* rely on fall-back browse vegetation.

The phylogenetic extreme hypsodonty evident for *A. bondi* suggests prolonged selective pressure to protect against a highly abrasive diet, such as grazing on new grass shoots with high silica content. Feeding on new shoots close to the ground also increases the likelihood of ingesting/masticating on exogenous dust/grit particles from the soil. Either of these elements, or particularly if combined, contribute to a highly abrasive content of the diet and would be a selective force for increased crown height.

This may explain the trend seen in *A. marsupialis* also. *A. marsupialis'* increase in crown height through time is likely due to an increase in an abrasive element in the diet, possibly an increase in grazing. From the comparatively low crown height of *A. recki*, *A. marsupialis* crown height progressively increases (from ~1.8 Ma onwards). An increased grass component, even seasonally, with more grassland present than was available for *A. recki* in the Pliocene would place an evolutionary pressure on the molars to increase capabilities to process the grasses as they gradually became a staple part of the *Antidorcas* diet.

If the preferred diet of *A. recki* is browse but their fall-back is to graze, and eventually more and more often they have to rely on their fall-back foods because of availability, the selective pressure acting on the molars would likely be to increase enamel thickness and crown height to withstand the abrasive properties of the monocotyledonous plants (If, ultimately, sufficiently adaptable to survive these selective pressures and changing environments).

Potential Inclusion of CAM Plants

A positive trend is apparent for carbon isotope $\delta^{13}C$ values and dental enamel thickness (Table 11.1). This may be expected as an increase in grass consumption would be more abrasive, selecting for increased enamel thickness to withstand the abrasive pressure; and

enhances $\delta^{13}C$ values with a C_4 vegetation dominated diet. This is supported by a negative correlation with oxygen $\delta^{18}O$ values (Table 11.1). As leaf consumption increases (evapotranspiration resulting in higher $\delta^{18}O$ values for browsing herbivores consuming leaves rich in $\delta^{18}O$), enamel thickness decreases.

However, this trend is only apparent for M^2. The other molars show the opposite trend for $\delta^{18}O$, with a positive correlation between $\delta^{18}O$ and enamel thickness. Alternative molars may reflect more of an interaction with the environment and $\delta^{18}O$ representing an increase in aridity. The positive correlation cannot reflect an increase in browsing leading to increased enamel thickness because the enriched carbon isotopes $\delta^{13}C$ values show increased grazing from the same individuals. This may implicate the inclusion of CAM plants, which mimic C_4 plants in their $\delta^{13}C$ values (Mooney et al. 1977; Codron et al. 2005; Sponheimer et al. 2013; Boom et al. 2014). Consuming CAM plants may be expected during periods of increasing aridity to obtain sufficient moisture (see Chapter 3), with the abrasive nature of CAM plants being unknown.

Whilst M^2 is most commonly used for analyses (e.g. Foretelius and Solounias), it would be more representative to conduct analysis on more than one tooth type to inform on how the molars differentially interact with their environmental and vegetation consumed and therefore, the inferences achievable from each tooth type. This is likely to vary between taxa.

Micro-Habitats

In a mosaic habitat landscape, with relative aridity that does not exceed an aridity threshold (so still supports C_3 plants), the impact of micro-habitats may be seen. The height of canopy cover at any given time is unknown but may be postulated based on other environmental indicators. Where taller trees (C_3) are present, the area underneath is more sheltered and less exposed to the heat of the midday sun. Typically, when these areas are close to a water body (e.g. river), this will be the last ground to dry up. Consequently, these areas would have increased moisture availability for plant evapotranspiration, sustained for a longer duration. If springbok seek shelter for thermoregulatory needs, they are likely to frequent these micro- habitats, particularly in a more arid regional environment.

The dietary signal resulting from this type of micro-habitat may be difficult to differentiate from a regional wetter environment. However, as it is unlikely that the assemblages are formed of one herd, the assemblage springbok would have moved independently of each other in life, and so, frequented differing micro-habitats. Within this dataset, such micro-habitats could be reflected in mixed feeding in individuals and across the species via the differing time scales shown through the dietary methods

In contrast, regional increased moisture would see these wetter habitats independent of tree cover. The individual animal and intraspecific dietary information is more likely to be uniform in a landscape sustaining a particular dominant habitat-type, where regional aridity levels and palaeoenvironmental conditions are prevalent throughout. That is, a savannah landscape with little to no tree cover and low precipitation levels would promote less ‘mixed-feeding’ from a variety of habitats and more uniform dietary indicators. In this

scenario, with exposed grassland, other than standing water, such as the river body (utilized more by obligate drinkers than by springbok), few wetter micro-habitat areas would be sustained.

Complementary Methods

The dietary proxies used here complement one another when all are used for one individual to assess lifetime dietary trajectory. From this, migratory patterns, seasonality and herd demographics can be considered in the fossil record in a way that would be invisible using a single method approach. Particularly by applying the differing dietary proxies to individual animals, the lifetime diet can be gained, this picks out if individuals are mixed-feeding at all stages of their life or switch from graze to browse. Comparing these individual animal signals with the signal obtained from the species and a genus as a whole, inferences can be made on a case by case basis as to the likely scenario, i.e. migration, seasonality or herd demographics.

Further, by comparing isotopes and use-wear analysis alongside dental measurements, particularly crown height and enamel thickness, inferences can be made regarding dietary abrasiveness and the selection forces acting upon the *Antidorcas* populations through time (as indicated above, see (Figure 11.1-Figure 11.45) This enables research to move beyond simple inferences from considering relative grazing versus browsing diets as a means to infer habitat types prevalent across the landscape.

Time-Averaging

By considering individuals, lifetime diet can be obtained for a small number of individuals within a time period. With the small sample sizes achievable here, this study is still limited by potential averaging when attempting to provide chronological patterns. With an increased sample size (beyond what can be conclusively achieved by this research), considering many individuals, utilising the same multiple methods on each, the issue of time-averaging could be substantially mitigated.

Seasonality

Seasonality could be reasonably inferred from the conflicting results obtained by the proxies representative of differing lifetime scales. The dominant diets for *Antidorcas recki* (browsing) and *Antidorcas bondi* (grazing) apparent from stable carbon isotope analysis, indicative of the early years of life differ from the lifetime (mesowear for both *A. recki* and *A. bondi*) and end of life (DMTA for *A. bondi*) dietary signals. Using multiple complementary methods, a simple conclusion of 'mixed-feeding' can be avoided, and the subtleties of *Antidorcas* diets can be accurately used to reflect seasonal palaeoenvironments. Strani et al. (2018) using use-wear analysis on Mid-Pleistocene bovids (Central Italy) also found a discrepancy between mesowear and microwear results. This was interpreted as a temporal switch towards a sub-optimal diet, possibly reflecting the effects of marked seasonality. Similar could be suggested here by the discrepancy between carbon isotopes, mesowear (grazing to mixed-feeding) compared to microwear (mixed-feeding to browsing) for *Antidorcas bondi*, particularly occurring for Swartkrans Member 2. Increased habitat heterogeneity and a shift towards more marked seasonality is suggested for Swartkrans Member 2 (c. 1.7-1.07 Ma) from the combination of dietary proxies used.

Feeding Height

The importance of determining feeding height influence, and related grit/dirt inclusion, shapes the accuracy of the palaeoenvironmental reconstructions achievable.

An attempt is made to determine the reasoning behind *A. bondi*'s conflicting results, both between methods used here and compared to some published research (e.g. Brink and Lee-Thorp 1992). A more comprehensive study, with larger sample sizes, is suggested for future research.

Modern *Damaliscus pygargus* is a low-level grazer (albeit presumably higher than *A. bondi* due to body size and with a wider muzzle). If for the purposes of this comparison, the assumption is made that the same was true for fossil *Damaliscus pygargus*; direct comparison of *A. bondi* and *D. pygargus* use-wear values could shed light on the cause of the values seen in *A. bondi*.

As both low-level feeders, the level of grit/dust inclusion should be roughly comparable (muzzle size and exact feeding height notwithstanding). As a known grazer (both modern and in the evidence here for fossil *D. pygargus*), any discrepancies between *D. pygargus* and *A. bondi* is likely a reflection of another factor other than exogenous particle inclusion. It may be presumed that factor is dietary, i.e. that *A. bondi* is not exclusively grazing, (or potentially the preferential plant taxa for *A. bondi* is developing herbivory defences differentially to other taxa preferred by species such as *Damaliscus*). Where the use-wear methods yield similar results, exogenous particles may be inferred as being the possible cause of values, such as more complex enamel facet surfaces (DMTA). Heterogeneity (HAsfc) and Tfv values are the most useful for inferring dietary flexibility here. High heterogeneity and Tfv for both *Damaliscus* and *Antidorcas* would support the inclusion of grit/dust. High heterogeneity for *Antidorcas* only would suggest *Antidorcas* was including more browse in the diet.

Table 11.10: Comparison of supplementary species (Damaliscus pygargus and Tragelaphus strepsiceros) with Antidorcas bondi averaged microwear and mesowear data to address feeding height, dietary and dietary abrasion questions. SK=Sterkfontein, K=Kromdraai, SKX=Swartkrans, GD=Gondolin, COH=Cave of Hearths. All values given to 2 decimal places. DMTA variables (Asfc, epLsar, HASfc, Tfv and Smc are in µm).

Taxon	**Provenance**	**N**	**Asfc**	**epLsar ($x10^{-3}$)**	**HAsfc[9]**	**HAsfc 81**	**Tfv**	**Smc**
T. strepsiceros	SK M4	1	2.03	3.33	0.39	0.60	37559.13	0.13
D. pygargus		1	1.90	3.21	0.27	0.60	34761.55	0.21
D. pygargus	SK M5	2	4.89	3.73	0.54	0.68	47498.62	0.14
A. bondi		5	2.34	2.35	0.25	0.59	45912.44	0.36
D. pygargus	KW	3	2.89	4.25	0.34	0.53	37028.65	0.35
T. strepsiceros		1	0.75	2.56	0.11	0.27	1598.83	0.53
D. pygargus	KE	1	2.33	2.15	0.63	0.60	41787.70	0.07
D.	KB	1	2.33	2.15	0.63	0.60	41787.70	0.07

Taxon	Provenance	N	Asfc	epLsar	HAsfc9	HAsfc	Tfv	Smc
pygargus								
D. pygargus	SKX M1	2	2.75	3.51	0.75	1.99	50324.24	0.17
A. bondi	KA	5	5.63	5.11	0.39	0.63	42470.00	0.09
D. pygargus	GDA	2	2.15	6.81	0.32	0.55	30466.43	0.35
A. bondi	SKX M2	23	5.91	2.26	0.39	0.72	40835.74	0.13
D. pygargus	SKX M3	3	1.46	2.34	0.23	0.52	35044.75	0.31
A. bondi		1	1.44	3.39	0.27	0.44	33149.02	3.00
D. pygargus	SK unstrat.	6	3.52	2.63	0.53	0.79	37618.84	39.25
A. bondi	COH	9	7.06	3.28	0.88	1.40	45289.08	0.75

Table 11.11: Damaliscus pygargus (left) (low-level grazer) and Antidorcas bondi (right) most frequently occurring (modal) mesowear scores for each deposit Member through time. SK=Sterkfontein, K=Kromdraai, SKX=Swartkrans, GD=Gondolin, PL= Plovers Lake, GL=Gladysvale, COH=Cave of Hearths.

Provenance	Upper/lower dentition	*D. pygargus*		*A. bondi*	
		N	Modal mesowear score	N	Modal mesowear score
SK M4	upper	1	LR	x	x
	lower	10	HR	2	LR
KB	Lower	3	HR	x	x
SK M5	upper	13	LR	14	LR
	lower	7	LR	12	LR
SK M5 E	upper	5	LR	x	x
	lower	9	HR	2	LS/HR
SK M5W	upper	5	LR	2	LB/LS
	lower	4	LR	4	LR
SK M5stw53	upper	1	HR	x	x
	lower	1	LR	x	x
SKX M1	upper	5	HR	x	x
	lower	1	LB	3	HR
SKX M1 LB	lower	1	LR	1	LR
SKX M1 HR	lower	x	x	1	LR
KA	upper	2	LR	3	LR
	lower	10	HR	9	LR/LS
GDA	upper	2	HR	x	x
	lower	11	HR	x	x
SKX M2	upper	2	LR/LS	42	LR/LS
	lower	4	LB/LR	42	HR
SKX M3	upper	5	LR	2	HR/HS
	lower	6	LR/HR	2	LR/HR
PL	upper	x	x	9	LS
	lower	x	x	6	LB/LR/LS
COH	upper	x	x	22	LR
	lower	x	x	20	HR
GL	upper	2	LR	x	x
	lower	7	LR	x	x
SK LC	Lower	1	LR	1	LB
SK un	upper	5	LR	x	x
	lower	5	LR	2	LB/LR
Modern	upper	67	LB	x	x
	lower	56	HR	x	x

Table 11.11 shows *A. bondi* marginally tends towards sharper cusps and more attrition-dominance than *D. pygargus*. As a low-level grazer *D. pygargus* typically shows abrasion dominated mesowear scores, characteristic of grazing bovid molars. From mesowear scores, *A. bondi* appears to include more browse vegetation in its diet, i.e. the browsing signal is not exaggerated due to low-level feeding- induced inclusion of grit.
Damaliscus pygargus does show a slight deviation from its normal mesowear score for Swartkrans Member 2, with sharper cusps. Coupled with the increased habitat heterogeneity and temporarily decreased aridity suggested from the *Antidorcas* data, *Damaliscus* tentatively (n=1 with sharp cusps, of n=2 total maxillary molars) supports Swartkrans Member 2 representing a transitional phase with temporary increase of browse vegetation, indicative of closed habitats and decreased aridity.

There are fewer comparative samples for microwear (DMTA) variables for *Damaliscus pygargus* and *Antidorcas bondi* (Table 11.10). However, where they can be directly compared for a member, they have very similar values, indicative of mixed-feeding to grazing diets. This contradicts findings from mesowear variables, showing the importance of considering results from multiple methodological approaches prior to making palaeoenvironmental assumptions. It also highlights the need for further study, with increased sample sizes for DMTA.

Damaliscus pygargus consistently shows grazing (abrasion-dominated) dietary patterns via mesowear variables. The same is true of DMTA variables. *A. bondi* shows grazing mesowear signals (low relief and rounded cusps dominating) for all members (where present) other than in Swartkrans Member 1 (high relief and rounded cusps dominate), Swartkrans Member 2 and Member 3 (equal high and low relief weighting, rounded cusps) and Cave of Hearths (high relief with 55% sharp cusps, 45% rounded cusps). From DMTA, *A. bondi* in Kromdraai A, Swartkrans Member 2 and Cave of Hearths, displays more complex enamel wear (i.e. higher Asfc values) than fossil or modern *Damaliscus pygargus*. The complexity values for Swartkrans Member 3 are very similar (Asfc for *A. bondi* (n=1) is 1.44 μm, for *D. pygargus* (n=3) is 1.46 μm). The epLsar values representative of anisotropy are typically lower for A. bondi than *D. pygargus*, other than for Kromdraai A (higher). Heterogeneity values were typically lower for *D. pygargus* (i.e. they were more homogenous) (range of: 0.25 μm Sterkfontein Member 5 – 0.39 μm Kromdraai A and Swartkrans Member 2), other than in Cave of Hearths, where they were considerably higher for *A. bondi* (0.88 μm HAsfc 9cell; 1.40 μm 81 cell) than typical values for *Damaliscus pygargus*, modern (0.65 μm 9 cell; 1.18 μm 81 cell mean) or fossil (ranges of: 0.23 μm Swartkrans Member 3 – 0.75 μm Swartkrans Member 19 cell; 0.52 μm Swartkrans Member 3- 1.99 μm Swartkrans Member 1 81 cell).

It is suggested that the apparent browsing for *A. bondi* is due to a combination of low-level feeding, incorporating exogenous particles to add to their dental use-wear signal, and of a more flexible diet of *A. bondi* (perhaps seasonally) than obligate grazing as seen in *D. pygargus*. By c. 0.5 Ma (Cave of Hearths), *A. bondi* exceeds the range of variation for low-

level feeding exogenous particle inclusion and flexible mixed-feeding, to exhibit mixed-feeding to browsing wear signals.

A fluctuation in increased exogenous particle inclusion is perhaps indicative of eolian dust increase. A larger sample size, with representation of *Damaliscus pygargus*, *Antidorcas bondi*, and other taxa of varying feeding heights (co-existing in the same temporal period / within the same assemblage) would be required to test this.

Palaeovegetation

The fresh grass shoots (prior to lignification) preferred by modern *Antidorcas* and suggested to be preferred by *A. bondi* (e.g. Brink and Lee-Thorp 1992) would be prone to leaving only shallow scratch imprints on dental enamel, vulnerable to overwriting (Solounias and Semprebon 2002; Hummel et al. 2010). Microwear (DMTA variables) do not support graze inclusion in the diet from the late Pliocene. It is possible that grasses were incorporated into the diet but their impact on the dental enamel surface (and visible via DMTA) was less than that of browse consumed.

That browse was consumed at all by *A. bondi* and apparently gradually increasingly through time for *A. bondi*, contradicts *A. bondi* exclusively belonging to a grazing succession. However, *A. bondi* could still have played a part in the succession, perhaps when grasses were seasonally available. Alternatively, *A. bondi* could have been involved typically in this grazing succession but was unable to consume preferred grasses at the end of life (DMTA). Where *A. bondi* in particular tends away from grazing signals as individuals (individual specimens), habitat heterogeneity can be inferred and as a species (overall signal from all *A. bondi* specimens within the assemblage), landscape-wide vegetation shifts can be inferred.

Similarly, C_3 grasses would leave fine scratches that are more likely to be invisible via DMTA. This presents an issue when questioning *Antidorcas* palaeoecology as grazing may occur but on C_3 grasses preferentially. Yet by utilising a multi-proxy approach, stable carbon isotope values, reflective of the relative C_3/C_4 components of the diet enable circumvention of this issue. However, the prevailing habitat (palaeoenvironmental) trend would prevail as mixed-feeding *Antidorcas* will consume the other C_3 vegetation within the habitat. Other C_3 vegetation, i.e. browse vegetation, leaves more substantial wear scarring, less prone to rapid overwriting, on the dental enamel, visible via DMTA. An inclusion of C_3 grasses in the diet *may* help to explain an apparently highly abrasive (usually associated with obligate grazing), yet mixed-feeding diet.

11.6 SUMMARY

Samples of different tooth types (toothrows and/ or multiple collections of isolated teeth) within a dataset are preferential to capture the full palaeoenvironmental signal.

Antidorcas Paleoecology

Mesowear *A. bondi* shows the most variable mesowear signals, with an indication for increased browse consumption for later deposits (c.0.8 Ma onwards). *A. recki* mesowear

indicates mixed-feeding practices, rather than browsing, and this is true throughout the temporal range. There are no obvious dietary transitions through time, for any *Antidorcas* species, apparent via mesowear alone.

DMTA *A. recki* is shown to be a variable browser. *A. bondi* displays a mixed-feeding to browsing microwear signature throughout. *A. marsupialis* is consistently mixed feeding, with no significant change through time.

Isotopes *A. bondi* yields a predominantly grazing signal from stable carbon isotope analysis; *A. recki* yields a predominantly browsing signal, and *A. marsupialis* a mixed feeding signal. All stable carbon isotope values support previous studies (e.g. Brink and Lee-Thorp 1992, Lee-Thorp et al. 2007).

Antidorcas recki was a predominantly browsing species; *Antidorcas* marsupialis was (and is) a variable mixed-feeding species. Dietary signals for *Antidorcas bondi* are conflicted, suggesting through time, periods of greater browse consumption than would be expected of this believed grazing (Brink and Lee-Thorp 1992) *Antidorcas* species. Mixed to browsing signals obtained for *A. bondi* for the last few days/weeks of life (via DMTA) coupled with the grazing early years signal (stable carbon isotope analysis), would suggest that either herd demographics dictate the young consume a greater amount of grasses; or that palaeovegetation changes resulted in consumption of non-preferred (or fall-back) foods for *A. bondi*. Assuming *A. bondi* was a preferential grazer (rather than ontogenically altering its diet), these palaeovegetation changes could result from palaeoenvironmental (abiotic) factors, leading to the reduction of grassland available for consumption; or an increase in competition (biotic factors) from more specialised grazers (although competition introduction could still be linked to palaeoenvironmental change).

Alternatively, the suggestion could be made that *A. bondi* were migratory, with the results shown here reflecting their relative local dietary habits. Grazing (isotope evidence) in the geographic area of lambing, grazing-mixed feeding (mesowear evidence) across the geographic range that they covered during their migrations and the browsing (microwear/ DMTA) reflecting the local palaeovegetation available around the Cradle of Humankind sites. The same logic could be applied to seasonality or herd demographics being reflected in the assemblage. Modern *A. marsupialis* mate and lamb opportunistically, following the rainy season, to take advantage of abundant (fresh grassland) vegetation. Such seasonality could be mirrored for *A. bondi*, utilising the fresh grasses as a newborn lamb (C_4 grazing dominance suggested from isotopes), variably consuming available foodstuffs throughout their lifetime (mesowear) but suffering in more challenging seasonal conditions, and therefore more likely to fall prey to predators/ death traps and the like, by having only non-preferential browse vegetation available for consumption at the end of life (DMTA). If herd demographics are being represented, the same would be apparent but sexual dimorphism may also be implicated through the adult years of life. Modern *A. marsupialis* does not show sexual dimorphism in dietary proxies, which supports an inference of seasonality/migration representation over herd demographics from the fossil assemblage.

Through Time

Measurements *A. marsupialis* crown height fluctuates through time (i.e. no directional increase/decrease through time), suggesting the forcing of dietary abrasives (fluctuations in grass (abrasive) availability and/or dust (exogenous abrasive particles).

A. bondi cusp height increases through time, from Sterkfontein Member 5, suggesting either an increase in grazing (or dietary abrasiveness), with increased cusp height to withstand this abrasive pressure. Alternatively, this could reflect an increased browse component of the diet, with occlusal/ cusp height closely linked to showing higher occlusal relief through time (via mesowear). As there are conflicting conclusions to be drawn from mesowear variables (as a method rather than here specifically), it is suggested that whilst *A. bondi* may be incorporating more browse in the diet through time, a highly abrasive mixed-feeding lifetime diet prevails.

Fluctuations in enamel thickness show no unidirectional trend through time for any *Antidorcas* species.

There is a high diversity of molar dimensions (occlusal aree and enamel thickness) for Sterkfontein Member 5, Swartkrans Member 2, Kromdraai A and Plovers Lake. These deposits represent c. 2.0-1.5 Ma. This diversity potentially infers a period of environmental instability.

Mesowear Swartkrans Member 2 shows the most variability and the most deviation from expected *Antidorcas* species dietary predictions. *A. bondi* shows the most variable mesowear signals, with an indication for increased browse consumption for later deposits (c.0.8 Ma onwards). There is no directional trend for any *Antidorcas* species through time for other palaeoenvironmental indicators (e.g. high relief and rounded cusps, indicative of increased annual precipitation (Kaiser and Schulz 2006), does not appear for any one member).

DMTA *A. recki* is shown to be a variable browser, with a slight increase in grass-consumption from Sterkfontein Member 4 to Member 5 and to Kromdraai W.

A. bondi displays an increase in browse-consumption apparent from Sterkfontein Member 5 (grazing to mixed-feeding) to Swartkrans Member 2 (browse-dominated).

Highly variable DMTA patterns for Sterkfontein Member 5 (1.7-0.8 Ma) and Swartkrans Member 2 (1.7-1.07 Ma) suggests increased habitat heterogeneity during these temporal periods.

From the *Antidorcas* DMTA data, mosaic landscapes with relative composition of habitats within the landscape being temporally variable are suggested between 2.8-0.5 Ma.

Isotopes *A. marsupialis* shows a gradual increase of browse consumption through time. Swartkrans Member 2 yields increased browsing signals for all species from stable carbon isotope values along with lower oxygen isotope values, potentially indicative of lower aridity.

Palaeoenvironments as Inferred from Combined *Antidorcas* Data

Sterkfontein Member 5 and Swartkrans Member 2 show more dietary variability, inferred to represent increased habitat heterogeneity and an increased woodland component compared to surrounding (earlier and later) deposits. The greater extent of habitat

heterogeneity initiated in Swartkrans Member 2 persists for subsequent deposits. For example, Swartkrans Member 3 shows greater habitat variability than Swartkrans Member 1. Whilst assemblages from 'Sterkfontein Member 5' could represent an extensive time period encompassing Member 5 Stw53 Infill, M5 East and M5 West, Swartkrans Member 2 is believed to be a single deposit. The increase in an abrasive element that is not definitively dietary, but is inferred as an increase in seasonal mixed feeding and/ or an increase in aridity (with associated increase in grass phytoliths). That is, whilst grazing may occur less frequently, the grass consumed is highly abrasive, potentially with the inclusion of abrasive exogenous materials (e.g. wind-borne dusts) associated with increasing aridity (as supported by oxygen isotope $\delta^{18}O$ values).

CHAPTER 12

DISCUSSION and CONCLUSION

Antidorcas dentition from South African hominin-bearing deposits spanning the temporal range of c. 2.8-0.5 Ma were analysed using a multi-proxy approach to establish the prevailing palaeoenvironmental conditions. The pace and severity of palaeovegetation change, has been inferred from *Antidorcas* dietary indicators (mesowear, microwear and stable carbon isotope analysis) and the impact of such change on *Antidorcas* (dental morphology directional change and intra-specific variability) was assessed. *Antidorcas* was used as an abundant, successful bioproxy (Sewell et al. 2019), from which to infer the palaeoenvironmental stimuli encountered by hominins during this temporal range. This mixed-feeding genus provided insight into the habitats available across the landscape; a landscape inhabited by hominins, for which the palaeoenvironmental signal had previously been elusive. The role played by global climatic changes that occurred through this time period, as evolutionary drivers, were evaluated by assessing *Antidorcas* dental morphological and dietary behavioural response across the proposed climatic events. The three main global climatic events during this temporal range are the intensification of the Northern Hemisphere Glaciation (iNHG) c. 2.7 Ma, the onset of the Walker Circulation (oWC) c. 1-9-1.7 Ma and the Mid-Pleistocene Revolution (MPR) c. 1.0 Ma.

This research has shown that across the Oldowan-Acheulean transition, and around the emergence of *Homo erectus* (*senso lato*) c.1.7 Ma, the global climate appears to be a prominent evolutionary catalyst, evidenced via increased habitat heterogeneity (high intra-specific *Antidorcas* variability in dental morphology and diet). Other global climatic events may hint at climatic influence but show relatively little evidence in the *Antidorcas* record of being critical evolutionary drivers.

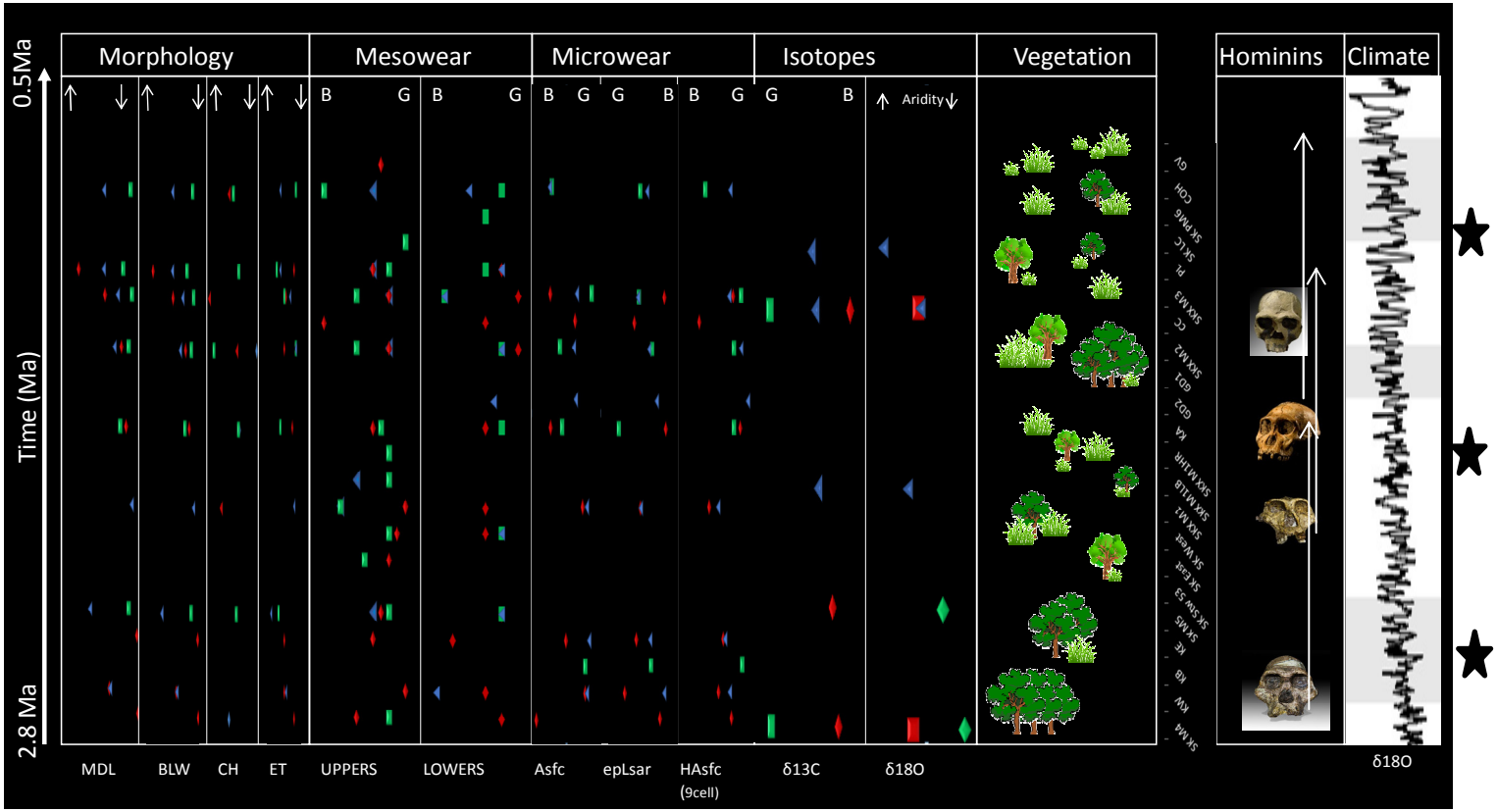


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Figure 12.1: Results of each method through time (y axis from c. 2.8 at the origin to 0.5 Ma) compared to hominin evolution and climatic fluctuations. Stars on the extreme right side of the image indicate the three major global climatic events that occur during this temporal range, from oldest to youngest: the iNHG, oWC and MPR (see glossary and chapter 2 'palaeoenvironments'). Climate data from benthic foramina $\delta^{18}O$ (‰) (deMenocal 2004; deMenocal 1995; Mix et al. 1995; Shackleton et al. 1990).

Results figure expanded explanation (Figure 12.1)
Data markers key: green = *A. bondi*, red=*A. recki*, blue= *A. marsupialis*. Upper arrow (left side of box) indicates larger size for measurements, lower arrow indicates smaller size. For isotopes, the lower arrow indicates decreased aridity (lower oxygen isotope value) on the right side of the box. 'G' indicates the grazing end of the dietary spectrum and 'B' the browsing end of the dietary spectrum. Carbon isotopes 'B' is indicative of C_3 vegetation dominance, 'G' of C_4 vegetation dominance.
Range for each method. Measurement (in mm) variables: MDL 12.11-16.3; BLW 8.2-13.71; CH 3.8-14.86; ET 0.7-1.13. Mesowear score (1-6) Grazing (G) (score 1, low relief and blunt cusps) to Browsing (B) (score 6, high relief and sharp cusps). DMTA variables: Asfc 1.79-9.22 μm; epLsar ($x10^{-3}$) 1.08-5.11 μm; HAsfc (3x3) 0.15-0.66μm. Carbon ($\delta^{13}C$) isotopes -1.09 to -11.17‰. Oxygen ($\delta^{18}O$) isotopes 26.55-33.91‰ (VSMOW).
Vegetation: The impact of environmental stimuli can be viewed via the extent and longevity of *Antidorcas* dietary shifts that occur between 2.8-0.5 Ma. A general trend of increasing aridity and a movement towards more open, grassland-dominated habitats through time, with some habitat heterogeneity throughout (mosaic habitats). Increased habitat heterogeneity with increased seasonality and lower aridity is evident c. 1.7 Ma.
Hominins show the species present. From the bottom upwards: *Australopithecus africanus*, *Paranthropus robustus*, *Australopithecus sediba* and *Homo erectus* (*senso lato*). Arrows extend from each hominin image to indicate their temporal range, *Australopithecus sediba* (FAD of c. 1.98 Ma) (Berger et al. 2010) has only been definitively found in one locale (Malapa Cave) and its range is therefore unknown.

Figure 12.2 (below) depicts the prevailing palaeovegetation trend inferred from all *Antidorcas* evidence from this research.

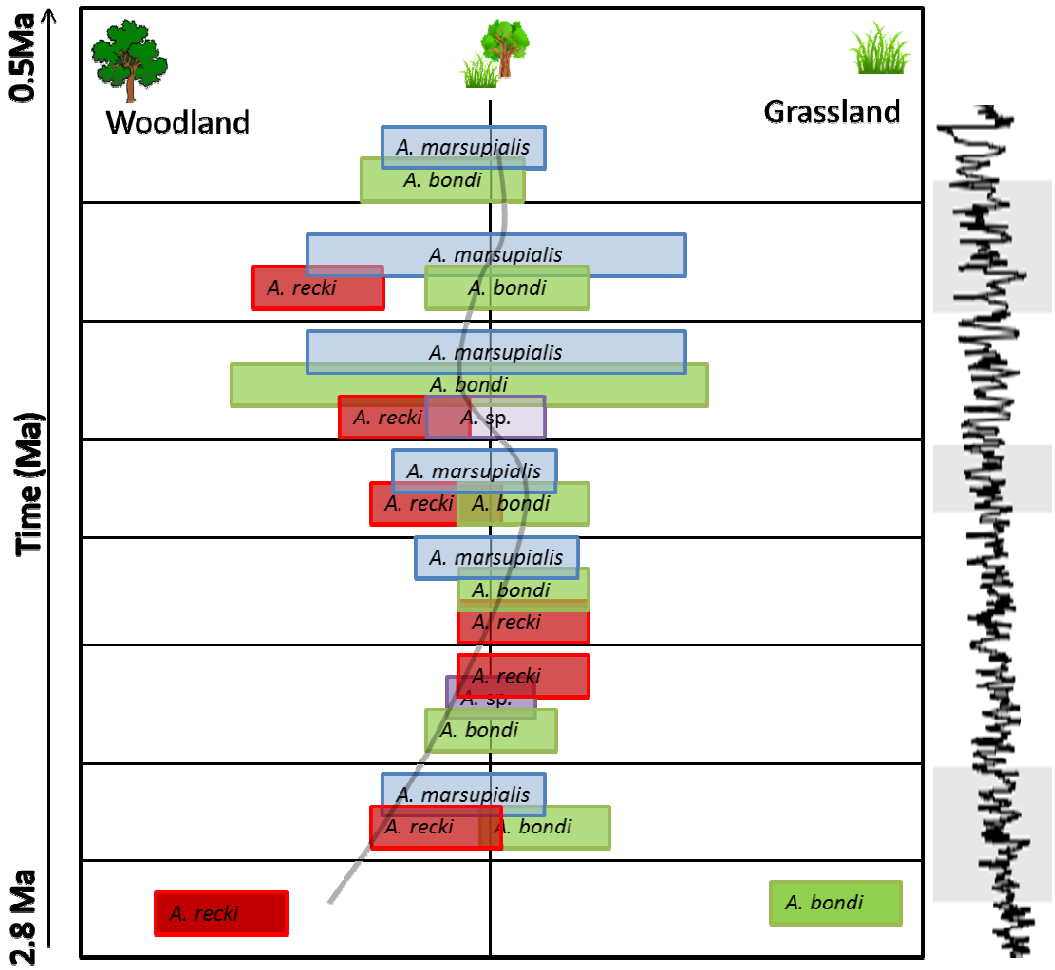

Figure 12.2: My interpretation of vegetation through time, inferred from Antidorcas dietary change. Based on Antidorcas species mean and individual lifetime diet (combined dietary signal obtained from all dietary proxies). The line represents the overall vegetation trend interpretation through time. Longer bars represent more intra-specific variation (individuals are lifetime grazers, browsers and mixed-feeders). 'Mixed feeders' are typically shown to be mixed-feeding to variable via all methods; or seasonal / lifetime mixed feeders (i.e. conflicting isotopes and microwear with mixed feeding signals via mesowear).

12.1 Summary of Results

12.1.1 MEASUREMENTS

- *A. marsupialis* crown height increases through time, suggesting the forcing of dietary abrasives (fluctuates in grass (abrasive) availability and /or dust (exogenous) abrasives).
- *A. bondi* occlusal height increases through time from Sterkfontein Member 5
- Fluctuations in enamel thickness (not unidirectional) apparent through time.
- High intra-specific diversity in Sterkfontein Member 5 (more so in M5 west), Swartkrans Member 2, Kromdraai A and Plovers Lake, environmental instability inferred.

12.1.2 Mesowear

- Swartkrans Member 2 shows variability and deviation from expected *Antidorcas* species dietary predictions.
- *A. bondi* is the most variable through time with increase in browsing signal (sharper cusps and higher relief) by later deposits (0.8 Ma onwards).

12.1.3 DMTA

- *A. recki* is a variable browser, with a small increase in grazing from Sterkfontein Member 4 to Kromdraai W and to Sterkfontein Member 5.
- *A. bondi* is mixed-feeding/ browsing throughout. Sterkfontein Member 5 (grazing to mixed-feeding dominates) and Swartkrans Member 2 shows browse dominated signal. These sites are considered roughly contemporary.
- *Antidorcas marsupialis* is consistently mixed feeding with no significant change through time
- Mosaic landscape with relative composition of habitats within being temporarily variable. Highest variability within Sterkfontein Member 5 and Swartkrans Member 2.
- From the late Pliocene, *Antidorcas* species do not graze (*senso stricto*) but are mixed-feeding/browsing, with any changes being marginal.

12.1.4 Isotopes

- *A. bondi* has C_4 dominance, grazing (with some mixed-feeding individuals)
- *A. recki* has C3 dominance, browsing (with some mixed-feeding individuals)
- *A. marsupialis* shows a gradual increase of C_3 consumption (browsing) through time
- Swartkrans Member 2 shows increased browsing signals (depleted carbon) for all *Antidorcas* species, alongside lower oxygen levels, indicative of lower aridity.

12.1.5 Multi-Method Comparisons

- A positive correlation exists between $\delta^{18}O$ and Tfv.
- A positive correlation exists between $\delta^{18}O$ both and $\delta^{13}C$ and enamel thickness (indicative of dietary abrasiveness).
- Unexpectedly, HAsfc (heterogeneity) negatively correlates with occlusal relief (linked to occlusal height measurements). More variable diets have lower relief and blunter cusps (for *Antidorcas* combined as a genus).
- EpLsar (anisotropy) and $\delta^{13}C$ positively correlate but unexpectedly, Asfc (complexity) and $\delta^{13}C$ also positively correlate, with a more depleted $\delta^{13}C$ value (associated with browsing) showing lower complexity (associated with grazing). This possibly indicates overwriting due to a highly abrasive diet, seasonal mixed feeding or DMTA variables reflecting fall-back foods.

12.2 *ANTIDORCAS* LINEAGE

A. bondi is more abundant in Swartkrans Member 2 and yet this is a period perceived to be more woodland dominated than surrounding Members. If reflective of the living community, this could be due to increased precipitation leading to growth of short grass shoots, the preferred diet of *A. bondi* (Brink et al. 1992). However, mixed diets are prevalent which may invoke seasonal migration inferences. Alternatively, this high abundance could reflect increased die-off of *A. bondi* during the temporarily more wooded, wetter environments and, or environmental instability during Swartkrans Member 2 deposition. *A. marsupialis* is found in increasing abundance from Swartkrans Member 1 onwards. *A. recki* is no longer found in assemblages after Swartkrans Member 3 (c. 1.5-0.61 Ma). On balance, *A. bondi* appears to be a seasonal migrant, with seasonal movements and lifetime dietary variability increases after c. 1.7 Ma, when the influence of seasonal changes becomes stronger.

Whilst it may appear to be semantics, identifying to species level prior to conducting dietary analysis has been shown to be of importance (e.g. Brophy et al. 2014; Sewell et al. 2019). *A. marsupialis* as a mixed feeder can be used to map vegetation changes where obligate grazers or browsers typically reflect their ecological preference. This research has shown all *Antidorcas* species to be more plastic in their diet than previous research (e.g. Brink and Lee-Thorp 1992; Lee-Thorp et al. 2007) suggests, with intra- and inter-specific variability ranges changing through time, presumably according to environmental changes.

12.2.1 Feeding Preferences of *Antidorcas* Species at The Cradle of Humankind

The presence of multiple *Antidorcas* species co-inhabiting the landscape, alongside other bovids of overlapping niche requirements (such as *Aepyceros melampus*) endorses the idea of high habitat diversity to support such a rich ecosystem. To conclude niche partitioning, one would have to determine to a greater degree of certainty that these individuals were deposited together, with temporal overlap of their inhabitation of the area, rather than representing different temporal (seasonal, glacial-interglacial, or otherwise episodic) deposition phases. Such clarity remains elusive at the Cradle of Humankind. Yet from this research, *Antidorcas* supports the notion of character displacement by increasing mixed-feeding through time, likely as a result of competition with specialists more suited to the expanding grasslands.

The successful use of multiple methods has allowed holistic dietary inferences to be made and in turn, the subtle complexities of the landscape to be untangled.

Antidorcas Paleoecology

From the late Pliocene, *Antidorcas* can be inferred as not grazing (*senso stricto*) in the last few days of the animals' lives (evidenced via microwear). Yet, *A. bondi* stable carbon isotope signals suggest otherwise and a highly abrasive diet (mesowear and dental measurements), particularly for *A. bondi* and increasingly through time for *A. marsupialis* appears prevalent. This either indicates seasonal availability of diet for all *Antidorcas* species, or seasonal

deposition, with deposition only occurring during wetter (browse-dominated vegetation) periods (e.g. Brain 1958, 1981, 1993, 1995; Pickering et al. 2007). Alternatively, the Cradle of Humankind could have fostered a local environment that was dominated by C_3 vegetation that the fossil springbok migrated into shortly before death. The latter scenario seems unlikely considering the wealth of references supporting opposing palaeoenvironments for the range of assumed *Antidorcas* migration (based on modern *Antidorcas* and migratory antelope ranges). A more plausible alternative is that a highly abrasive diet masked (overprinted) any grazing signal from the microscopic wear evident on the dentition. The results of this research show that all *Antidorcas* trend gradually towards an increased C_3 component in their diet, the opposite of what may be expected from an increasing grassland trend through time. This is perhaps due to character displacement imparted on *Antidorcas* from more specialized grazers as grassland habitats expanded.

This research has shown *Antidorcas marsupialis* increase in dental crown height through time, which is interpreted as an adaption towards a more abrasive diet, either due to an increase in eolian dust (incorporated into the mouth whilst low-level feeding) or as a response to increased inclusion of abrasive grasses as savanna grasslands expanded and aridity increased. This is supported by abrasive mixed feeding diets suggested by mesowear signals, which are indicative of the lifetime selective influences acting upon the individual animal and upon the species.

Antidorcas bondi

The results presented in this thesis (stable carbon isotopes, extreme hypsodonty) go some way to supporting *Antidorcas bondi*'s preference for grazing. Yet the signal obtained by using a combination of methods (mesowear, DMTA) is not as clear as may have been anticipated (e.g. based on Brink and Lee-Thorp 1992's isotope study). Although primarily believed to have been a grazing species, as evidenced from previous stable isotope analysis (Brink and Lee-Thorp 1992; Lee-Thorp et al. 2000; Codron et al. 2007; Sewell et al. 2019), my analyses show more mixed–feeding, which implies greater intraspecific dietary variability. Mixed-feeding is further supported by evidence from Cornelia (1.07-0.99Ma) (Brink et al. 2012), Florisbad (0295-0.225 Ma) (Herries 2011), Haasgat (c. 2.2-2.0 Ma) (Adams et al. 2013) and from this study, which implicates the possibility of greater intraspecific dietary variability. *A. bondi* is predominantly grazing but with a higher C_3 component in its diet than would be anticipated based on previous studies (e.g. Brink and Lee-Thorp 1992), and appears to increase the browse-component intermittently, with a gradual trend towards increased browse. Thus, the presence of *A. bondi* should not be used as a reliable indicator of grassland presence.

A. bondi is believed to have fed on the new grass shoots close to the ground, working sympatrically with other species in a grazing succession. The larger animals mow the sward at higher levels, leaving the smallest new growth shoots for the smallest in the succession, *A. bondi* (see chapter 3 'fossil *Antidorcas*'). The low-level feeding height would inevitably encourage more grit consumption. This would be particularly true of a wide-muzzled antelope. If a shortening in width of the incisor teeth (not measured here) occurred through time, this may

provide further insight into the evolutionary pressure that this type of feeding enacted on *A. bondi*.

A low **feeding height** and the incorporation of high levels of grit from feeding close to the ground would result in a highly abrasive diet. This would explain 'browsing' diets yielded via microwear analysis, yet abrasive microwear and mesowear signal. Taken alongside the grazing isotope signal and extreme hypsodonty (selected to withstand the abrasive grass phytoliths and grit), these combined results support *A. bondi* being, at least for some of the year, a low-level grazer as part of a grazing succession, or low mixed-feeder, including grasses.

The signal here indicates a combination of both increased browse-consumption and increased grit intake. The cusp height increase apparent in *A. bondi* after c. 1.7 Ma-0.8 Ma (Sterkfontein Member 5) suggests an increase in dietary abrasiveness just prior to/ during this temporal period. Thereby forcing selective adaptation measures to allow *A. bondi* to withstand the abrasive pressure. An alternative scenario is supported (primarily) by mesowear results, of a reduction in abrasive material (grass phytoliths or exogenous particles) and a likely replacement with increased browse consumption on an individual lifetime scale. If the latter is true, this could reflect vegetation change, with a reduction in preferential grasses; this scenario is supported by mesowear results. If so, the environmental change caused by the onset of the Walker Circulation (c. 1.9-1.7 Ma) could be implicated here.

A. bondi shows the most variable mesowear signal through this temporal period of any *Antidorcas* species. An increase in browse incorporation in the diet is evidenced via a gradually increasing occlusal height and associated browsing mesowear signal through time from Sterkfontein Member 5 [c. 1.8-1.1 Ma (based on ESR and palaeomagnetism dating techniques)].

Coupled with the end of life (microwear) mixed-feeding to browsing signal, it is concluded that *A. bondi* had a highly abrasive, mixed-feeding (likely seasonal mixed feeding) diet, with a gradual increase in browse through time.

Antidorcas recki

East African *A. recki* c. 1.7 Ma (Olduvai Gorge, Tanzania) was interpreted (using a similar mixed methodology approach) as a seasonal mixed feeder (Rivals et al. 2018). Yet such a detailed approach for South African *A. recki* was previously missing.

The results from this research (stable isotopes and use-wear) demonstrate South African *Antidorcas recki* was predominantly a variable browsing to mixed-feeding species. A slight increase in grass consumption is evident (via microwear) from Sterkfontein Member 4 (c. 2.8-2.0 Ma) to Member 5 (1.8-1.1 Ma) and to Kromdraai W (between Sterkfontein Members 4 and 5). The lifetime signal from mesowear analysis shows *A. recki* to have been a mixed-feeder. Combining this with the browsing dominance (evidenced from isotope analysis) and the variable browsing with steadily increasing grass consumption (evidenced via microwear), seasonal mixed-feeding could also be inferred here. Shortly after 1.5 Ma, *A. recki* disappears

from the fossil record. This is likely to be linked to increased environmental instability and character displacement (see Appendix A5 for further discussion of *A. recki* extirpation).

Antidorcas australis

This research does not support *A. australis* being distinguished as a separate species found in the Cradle of Humankind during this temporal range. *A. australis* could potentially be present as *A. m. australis* (i.e. a sub-specific population). Alternatively, *A. australis* as a distinct species could have existed as a Cape endemic. From dental morphology alone, the Cradle of Humankind specimens potentially identified as *A. australis* do not show enough variation from the other *Antidorcas* species, particularly *A. marsupialis* to warrant separate species status.

This research therefore incorporated potential *A. australis* specimens, largely within *A. marsupialis*. Occasionally, some proposed *A. australis* specimens were reassigned as *A. recki/A. bondi* based on morphological identification criteria, and often supported by previous researchers (e.g. de Ruiter 2003) (see Chapter 6 'Taxonomic identification of species' for individual specimen details). The need for taxonomic clarity has been demonstrated in this research.

Antidorcas marsupialis

These results demonstrate *Antidorcas marsupialis* was predominantly a mixed-feeding species, from all methods applied, with a gradual increase in the browse component of the diet through time.

No clear FAD (first appearance date) is apparent for *A. marsupialis* from the dietary and habitat information gained through this research. Any dramatic increase in variability followed by morphological change may be suggestive of speciation to *A. marsupialis*. Yet the overlap between all *Antidorcas* species throughout the fossil record and comparatively with modern *A. marsupialis* renders the FAD of *A. marsupialis* difficult to determine.

As an abundant antelope present in many hominin-bearing deposits, the ability to accurately interpret and utilize *Antidorcas* remains effectively is beneficial. Therefore, a better understanding of their anticipated levels of variation, as extrapolated back from their modern counterparts is of importance. This research has established the range of variation of modern and fossil *Antidorcas* as a genus, which could usefully be compared to other *Antidorcas*-bearing sites.

Modern *A. marsupialis* have been witnessed practicing geophagy, actively consuming soils and natural 'licks'(clay soils, often near waterholes) to supplement their nutrient intake, often in arid environments (e.g. Bigalke 1972; Stapelberg 2007; Stapelberg et al. 2008) or counteract the toxic effects of plant secondary compounds (Damuth and Janis 2011). If the same were practiced by fossil *Antidorcas*, this may present as an abrasive diet (due to the inclusion of exogenous grit from actively consuming soil/ dirt particles) and increased wear complexity (DMTA). An inflation therefore, in increased dietary abrasion and greater wear complexity (often concluded to be a browsing signal), as seen in Swartkrans Member 2 for instance, could reflect the dependence on such fallbacks. This could suggest *Antidorcas* is unable to obtain

required nutrient levels from vegetation consumption alone and other considerations should be noted when using *Antidorcas* materials for similar research questions.

As mentioned, geophagy is also practiced to counteract the toxic effect of secondary compounds in plants (as the plants' defence against herbivory) (e.g. Pfister 1999; Ayotte et al. 2006). During periods of high energy demand (e.g. rutting, lactating), vegetation consumption would increase. Therefore, increasing the use of natural licks/ soil consumption to counteract the effects of toxic secondary plant compounds (e.g. Voigt et al. 2008), and hence the likely seasonal increase in exogenous particle inclusion. Similar behaviour was found for modern moose utilizing sodium licks seasonally according to salt (sodium) requirements (Fraser et al. 1982). An increase in dental abrasion, particularly if combined with browse signals should consider this as a possibility. From this research, it is likely that the *A. marsupialis* and *A. bondi* inference of increased seasonal behaviour differentiation and dietary abrasion after Swartkrans Member 2 incorporated similar practices.

12.3 PALAEOENVIRONMENT OF SOUTHERN AFRICA

12.3.1 Regional scale

A meta-analysis of South African hominin bearing locales (chapter 5), combined with the *Antidorcas* data suggest that varying mosaic habitats (Reynolds 2010) of shifting woodland and grassland components in the landscape are prevalent throughout this temporal range. The general trend from woodland dominance to grassland dominance is apparent and increased environmental instability and seasonal differentiation inferred from c. 1.7 Ma. The *Antidorcas* palaeoecology evidence discussed in the previous section is used to make this inference, with the implications for the palaeoenvironment discussed further here.

The diversity that emerges in Swartkrans Member 2 (and to a lesser extent in Sterkfontein Member 5) via dietary evaluation of *Antidorcas* is not mirrored in the faunal assemblage (via cluster analysis of faunal assemblages, see chapter 5) across southern Africa. However, this meta-analysis was conducted on presence / absence data, the relative abundance of fauna may still reflect increased biodiversity for Swartkrans Member 2.

A. bondi's presence and grazing diet in Sterkfontein Member 4 supports the notion of open, grassland habitats to the landscape already a component of the landscape by ~2.8-2.5 Ma (e.g. Avery 2001; Avery et al. 2010; Elton 2001; Luyt 2001; Luyt and Lee-Thorp 2003; van der Merwe et al., 2003). With *Antidorcas* evidence supporting grassland habitats making up a lesser component of the mixed habitat landscape than in later time periods.

Turner's (1985) suggestion of seasonally deposited *A. bondi* specimens, restricted to the summer months, due in most part, to the apparent absence of juveniles is interesting. This scenario would corroborate with the suggested fluvial action aiding cave deposition (Brain 1958, 1981, 1993, 1995; Pickering et al. 2007) and the inflated browsing signal obtained via DMTA here. The summer months have higher rainfall on average, enabling surface deposits (such as leopard kills) to be introduced to the cave, as well as supporting the growth of vegetation preferring wetter environmental conditions. However, it is suggested here that *A.*

bondi has a highly abrasive diet, as such; juveniles may be falsely mis-recorded as older individuals due to the excessive wear caused by their highly abrasive diet. If juveniles are not actually absent from this deposit, Turner's (1985) argument loses its key evidence.

Supposing extant *A. marsupialis* can be used as a reliable model for extinct *A. bondi*, *A. marsupialis* is traditionally a summer grazer and winter browser (Kingdon 1997). Based on the evidence available here (rather than on inferred assemblage demographic profiles) one might anticipate increased grazing DMTA signal (low complexity and high anisotropy) and/ or perhaps increased C_4 isotope signals, to indicate deposition restricted to the summer months. Palaeoecology is rarely that straight forward however, and as alluded to previously, DMTA may confuse signals by inflating browsing signals from a 'micro'-climate (micro on an *Antidorcas* scale), whereby a small refuge type area is sought for shelter and to find more moisture-rich vegetation, during the more arid months. This is also the preferred habitat type of *A. bondi*'s believed, key predator, the leopard (*Panthera pardus*). Thus, although DMTA does not conclusively indicate grazing-dominance for *A. bondi* (so one may be opposed to inferring summer months based on extant *A. marsupialis* seasonal dietary habits), *A. bondi* may actually have been more prone to being driven to these areas during the summer months and therefore, the assemblage may still be inferred as seasonally deposited during the summer months. Moreover, *A. bondi* may have been outcompeted by *A. marsupialis*, with niche partitioning forcing A. *bondi* to an increased browse component during the summer months when *A. marsupialis* is believed to prefer increasing the graze content of its diet (if basing fossil *A. marsupialis* dietary palaeoecology on modern *A. marsupialis* dietary ecology).

Either way, the issue of seasonality of fossil *Antidorcas* movements (seasonal migrations) and of seasonal deposition is an essential consideration prior to inferences being made from the dataset.

That isotope signals differ from microwear signals and that mesowear is extremely mixed in the majority of cases supports the notion of seasonal migrations of fossil *Antidorcas*. Whilst this restricts inferences obtainable about palaeoenvironments local to the Cradle of Humankind, regional observations prevail.

The alternative inference is of feeding height. Although fossil *Antidorcas* differed slightly in body size, and modern *A. marsupialis* is known to occasionally feed at a higher level, *Antidorcas* is suggested to be a low-level grazer (e.g. *A. bondi* Brink and Lee-Thorp 1992; Brink 2016). The disparity in results from differing methods may actually not show different feeding through life but rather be indicative of a low-level feeding practice. With increased dust/grit consumption a likely consequence of feeding at low levels. Dust/grit has been shown to be a dietary abrasive, evident on dental molar wear (Lucas et al. 2013; Wood 2013; Xia et al. 2015), although studies have shown grit/dust does not impact as much as diet on microwear (e.g. Merceron et al. 2016), the impact of such particles may be key in this instance. The highly abrasive diet known for *A. bondi* through mesowear, as well as perhaps the increased

heterogeneity and complexity of the microwear scarring could be indicative of high levels of grit consumption.

Precipitation levels would need to be relatively high to sustain *A. bondi* in this dietary habit, to ensure the grasses have sufficient water to remain in a state of regrowth and fulfil the nutrient requirements of the antelope (Brink 2016), *A. bondi*. Oxygen isotope values from Swartkrans Member 2 suggest increased precipitation, which is when *A. bondi* is found in great abundance. However, the trend of gradually increasing aridity through time may also be responsible for enhanced dust prevalence, carrying and depositing increased quantities of eolian dust across the landscape. Increases in African wind-borne dust occur after 2.8 Ma, with peak values around 1.9-1.6 Ma off East Africa (deMenocal 2011). The dust-rich palaeoenvironments in which *Paranthropus* lived, contemporaneously with many of the *Antidorcas* considered here, particularly Swartkrans Member 2 *A. bondi* (and *A. marsupialis*) have been causally linked to an increase in *Paranthropus* enamel thickness (Lucas et al. 2013). Exogenous particles (dust/grit) were considered to be responsible for driving these abrasion-resistance adaptations (Madden 2014). The *Antidorcas* data here supports this hypothesis.

Measurements show that dental enamel thickness and occlusal volume (see chapter 11 'multi-method analysis') for *A. bondi* differs significantly between Swartkrans Member 2 and Sterkfontein Member 5, which are considered roughly contemporary, suggesting the impact of micro-scale influences, such as the increased consumption of moisture-rich vegetation supported closer to Swartkrans (due to its proximity to the Blauubank river), compared to Sterkfontein. However, Sterkfontein and Swartkrans were likely within the home range of *A. bondi* and its predators, so this difference may be better interpreted as temporally distinct populations and, the apparent difference of 'contemporary' populations an artefact resulting from time-averaging of deposits. As stated above (section 12.2.1), *A. marsupialis*' increase in crown height through time supports increasing aridity and expansion of grasslands.

Lifetime diets evidenced via **mesowear** reflect mixed-feeding as evident for all *Antidorcas* species. *A. recki* reveals more inclusion of grass in the diet, or a highly abrasive lifetime diet, than is suggested via microwear or stable isotope analysis. *A. bondi* again shows mixed-feeding to variable grazing or a highly abrasive mixed feeding diet throughout, with a tendency towards increased browse by 0.5 Ma. *A. marsupialis* shows mixed-feeding with more intra-specific variation than the other *Antidorcas* species. Therefore, mixed, or seasonally fluctuating, habitats are inferred throughout. Less emphasis is placed on mesowear results compared to the other methods as further parameters are required to ensure accurate palaeoenvironmental and dietary indications.

Microwear data shows no significant difference between *Antidorcas* species, other than in Swartkrans Member 2. All *Antidorcas* species from the late Pliocene are mixed-feeding to browsing at the end of their lives. A very small number of individuals within each species show grazing-dominance. Highly variable DMTA results are gained inter- and intra- specifically for *Antidorcas* for Sterkfontein Member 5 (c. 1.7-0.8 Ma) and Swartkrans Member 2 (c. 1.7-1.07

Ma). Woodland habitat presence is inferred as being available throughout, with a period of habitat heterogeneity c.1.7-0.8 Ma.

Carbon isotope ($\delta^{13}C$) values may reflect vegetation away from the Cradle of Humankind if *Antidorcas* were migratory during the Plio-Pleistocene. *A. bondi* has a C_4 plant, graze dominated diet until Swartkrans Member 2, (c. 1.7 Ma), after which mixed-feeding, likely seasonal, dietary preference is apparent. *A. recki* typically shows a browsing diet, with 2 individuals from Swartkrans Member 1 displaying a mixed-feeding (mixed C_3/C_4) diet. *A. marsupialis* typically shows mixed-feeding via carbon isotope analysis, although one individual in Swartkrans Member 2 shows grazing (C_4) dominance, three individuals show browsing (C_3) dominance and one individual a mixed-feeding diet, supporting an inference of habitat heterogeneity and /or environmental instability for c. 1.7 Ma.

Oxygen isotopes are perhaps more difficult to accurately interpret via a water-independent mixed feeding taxa. High oxygen $\delta^{18}O$ values can be indicative of browsing diets, with browsers consuming leaves richer in oxygen than lower parts of the plant due to evapotranspiration. Alternatively, higher $\delta^{18}O$ values could be indicative of increased aridity levels, with transpiration occurring more rapidly in C_4 plants under arid conditions. Combining oxygen isotope values with carbon isotope values makes this differentiation more readily identifiable. The prevailing trend is one of gradually increasing aridity from c. 2.8 Ma to 0.5 Ma, with a period of reduced aridity c. 1.7-1.5 Ma, alongside some evidence of enhanced seasonal differences in precipitation from c. 2.0-1.5 Ma onwards. The seasonal divergence is inferred from more frequently occurring discrepancy between carbon isotope ($\delta^{13}C$ enrichment at the start of life) and microwear variables (at the end of life) for individuals, alongside intra-specifically variable $\delta^{18}O$ values.

As acknowledged by Luyt (2018), *Antidorcas'* mixed-feeding diet aligns more closely with that of habitual browsers and therefore, may represent the minimal grass component of the landscape.

Fire

A prominent part of modern savanna biomes is the repeated disturbance by fires. The likelihood of fire is influenced by vegetation traits, with fire being more likely in areas with high light (little to no canopy cover) and high productivity (Lehmann et al. 2011). A C_4 grassland dominated landscape permits fire (due to the light exposure and higher aridity compared to C_3 closed canopy habitats). The fire then promotes C_4 grasses by maintaining an open canopy, initiating a positive feedback system between savanna grasses and fire (Beckage et al. 2009).

The impact of fire / wildfire would be difficult to determine from time-averaged cave deposits but the possibility of their impact upon the local vegetation and the fauna inhabiting it, remains. However, modern *A. marsupialis* consume *Acacia* species (Skinner and Louw 1996, Figure 12.3), which are known to tolerate, and potentially benefit, from repeated burning. New acacia shoots regrow in the first months of the wet season but photosynthetic rates of the acacia remain high into the dry season months (enabling root starch replenishment) (Schutz et al. 2009). The

new shoots are extremely responsive to CO_2 levels, which impact upon their water-use efficiency and photosynthesis rates (Drake et al. 1997).

Thus, we might expect an increase in fire disturbance correlated to the expansion of savanna C_4 grasslands. C_3 trees are fire resistant if a fire occurs (C_3 grasses are destroyed) but C_4 grasses promote the initiation of fire and can rapidly repopulate following the disturbance, given the right environmental conditions (low but seasonal rainfall) (Lehmann et al. 2011). The frequency of fire disturbance dictates the long-term landscape cover. Frequent fire support C_4- dominated savanna habitats, whereas C_3 vegetation is able to outcompete and re-establish in the absence of disturbance (e.g. Archibald et al. 2009; Lehmann et al. 2009).

In the fossil record, the possibility that either an aridity threshold was reached that resulted in wildfire, or that wildfire occurred from lightning strike may be relatively invisible. In this instance, particularly if these fires were prolonged or rapidly repeated, C_3 plants (larger trees), which are more fire-resistant (Bond and Midgley 2012) would temporarily prevail and/or be supported alongside dominant grasses in a savanna landscape. For instance, Swartkrans Member 2 *Antidorcas* appears to be depleted in carbon (interpreted as an increase in browse) and lower oxygen isotope values (indicative of less arid conditions). From Member 2 onwards, increased habitat heterogeneity (and mixed savanna landscapes, such as those encouraged by fire disturbance) is inferred. In the subsequently deposited Member 3, evidence of repeated burning is apparent, interpreted by Brain and Sillen (1988) as hominin-controlled fire.

Modern wildfires are typically characteristic of seasonally wet savannas, with the vegetation present being more tolerant to fire (Bond and Midgley 2012). With the proposed increase in seasonality c.1.7 Ma, and a likely period of environmental instability (c. Swartkrans Member 2), repeated wildfires could tentatively be a possible alternative explanation to hominin-controlled fire (Swartkrans Member 3).

Figure 12.3: Modern springbok eating acacia (Image from L'univers fascinant des a nimaux, Le Springbok, (ISBN : 2-908306-07-7) ©MCMXCIII IMP Sarl/IMP BV, Groupe 1, Fiche 176).

Antidorcas could provide more valuable insight into the impact of fire on the palaeovegetation around this temporal range. With further research into the dental use-wear acacia inflicts on dental enamel, the carbon isotope composition of *Acacia* and investigation into the impact of fire on the carbon and oxygen isotopes of these plants (and the differential seasonal signal).

12.3.2 Local scale: Cradle of Humankind sites

Swartkrans supports more of a continuous faunal community than Sterkfontein (see chapter 5, 'Meta-analysis'), this is perhaps due to local or micro-scale buffers, allowing Swartkrans to retain habitats whilst Sterkfontein is more vulnerable to climatic or otherwise environmental variability. Sterkfontein Member 5 west, (which shows high habitat diversity (from the A*ntidorcas* evidence) compared to other Sterkfontein Members) support similar taxa to

Swartkrans. The local buffers (e.g. proximity to the Blauubank river) inferred for Swartkrans (see chapter 2) were perhaps sufficient to withstand typical climatic stimuli but did not dampen the impact of the regional environmental change evident from c. 1.7 Ma.

12.4 POTENTIAL IMPLICATIONS FOR HOMININS

The *Antidorcas* data therefore indicates the landscape was increasingly dominated by savanna landscapes, supporting both woodland-type habitats (C_3 vegetation) and open grassland (C_4 vegetation). This would support multiple hominin species with specialized or flexible diets, as with *Antidorcas*. The environmental instability inferred around Swartkrans Member 2 would likely favourably have reduced numbers of dietary specialists of all taxa (*Antidorcas* and hominins).

Although typically, the impact of climate is overshadowed in East Africa, climate variability (c. 1.8-1.7 Ma) in West Turkana, as evidenced via leaf was biomarkers (Lupien et al. 2017, 2018) has been suggested to select for adaptability and drive hominin evolution. Similarly, the evidence from *Antidorcas* dentition supports this notion in South Africa also. This primarily supports the variability selection hypothesis (Potts 1998) and the environmental variability selection hypothesis (Maslin et al. 2014, 2015).

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Table 12.1: Hominin evolutionary events within this timeframe that have been casually linked to environmental or climate change catalysts, alongside whether or not this is supported by the environmental picture gained from the Antidorcas evidence here

Date	South African Event	Hominins present in South Africa	Previously proposed environmental catalysts	*Antidorcas* support?
c. 2.0 Ma	Appearance of *P. robustus*	*P. robustus,; A. africanus, A. sediba*	Woodland habitats and wetlands. High climate variability.	Little support. Mixed feeding diets and low indication of increased variability from SK M5.
2.8-0.8 Ma	Co-occurrence* of hominins	*P. robustus, A. africanus, A. sediba, Homo sp.*	Habitat heterogeneity and proposed niche partitioning; adaptation to a more arid, varied environment.	Support. Co-occurrence* of *Antidorcas* species with niche partitioning, dietary and habitat generalization evident.
c. 2.0-1.8 Ma	Disappearance of *A. africanus*		iNHG/oWC. High climate variability.	Little support. Mixed feeding diets and low indication of increased variability from SK M5.
c. 1.9-1.7 Ma	Appearance of *Homo erectus* (*senso lato*)	*Homo* sp., *P. robustus,*	oWC, High climate variability.	Support. Environmental variability (supporting Potts 1996,1998; Maslin et al. 2015)
c. 1.7-1.6 Ma	Oldowan-Acheulean tool technology advancements	*P. robustus, H. habilis, H. erectus (senso lato*)	oWC (and consequent seasonal variation and environmental instability experienced).	Support. SKX M2 and SK M5W (1.7-1.07 Ma) high intra-specific variation in dental morphology and behaviour; increased habitat heterogeneity from this… …time and (with the highest degree of variability experienced in SKX M2 around the onset of change).
c. 1.0 Ma	Controlled use of fire	*H. erectus* (*senso lato*)	Behavioural advancement	No support. *Antidorcas*

Date	South African Event	Hominins present in South Africa	Previously proposed environmental catalysts	*Antidorcas* support?
			of *Homo* genus due to above catalysts.	evidence suggests potential for wildfires which could negate the controlled use of fire by hominins.
c. 1.0Ma	Disappearance of *P. robustus*	*H. erectus* (*senso lato*)	MPR, marked precessional variability; expansion of savanna grasslands	Support. Disappearance of *A. recki*

* Time-averaging notwithstanding.

12.4.1 Oldowan-Acheulean transition around the Cradle of Humankind

In East Africa, the consideration that the palaeoenvironmental change across this transitionary temporal range may have more implications than simply hominin (*Homo ergaster/erectus*) emergence has been recently investigated (e.g. Uno et al. 2018; Prassack et al. 2018). *Homo habilis* and *Paranthropus boisei* were still present during this time and the shift in lithic technology may be a response to the shifting environmental conditions rather than a different species (*H. erectus*) as the manufacturer of the Acheulean, as is traditionally assumed. However, no large-scale environmental shifts were found in this region by either avifauna (Prassack et al. 2018) or mammalian fauna (Uno et al. 2018). In southern Africa, *Paranthropus robustus* and potentially *H. habilis* (see Clarke and Howell 1972; Kuman and Clarke 2000; Albarède et al. 2006; Smith and Grine 2008; Curnoe 2010; Wood 2014; McKee 2017) are also present during this temporal overlap.

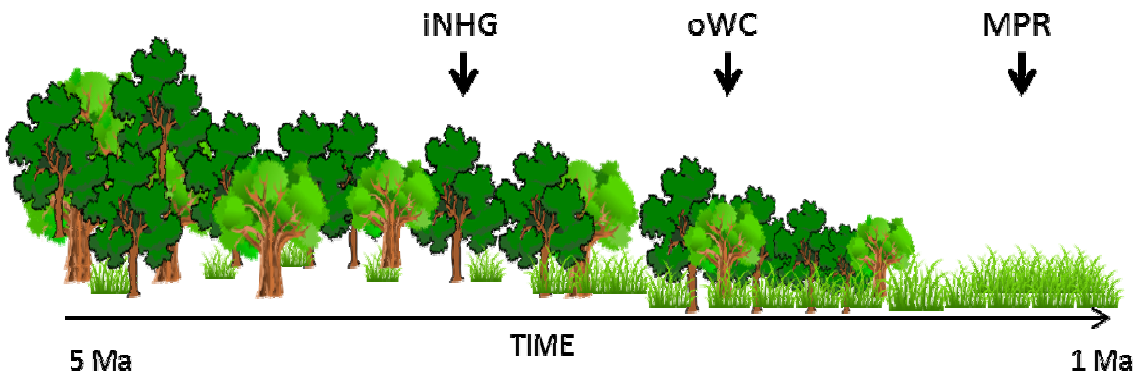
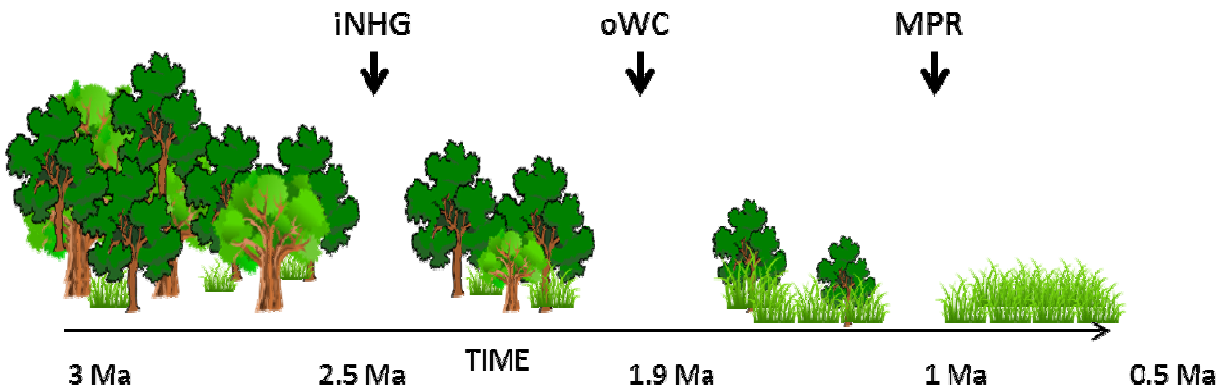
In the central interior of South Africa, as represented by the hominin-bearing site of Wonderwerk, local factors (the impact of regional rainfall seasonality and carbon dioxide (CO_2) levels appear to dictate vegetation cover contrastingly to the East of southern Africa (Cradle of Humankind) and of Africa (Kenya, Ethiopia, Tanzania). The evidence from Wonderwerk suggests prolonged wetlands supported both C_3 and C_4 grasses through the Early Pleistocene and no definitive trend towards aridity was prevalent during the Oldowan-Acheulean transition as has been postulated for other hominin-bearing sites (Ecker et al. 2018).

In the Cradle of Humankind, some degree of habitat heterogeneity is supported throughout this temporal range, with woodland habitats slowly declining through time. The suggested environmental instability and habitat heterogeneity for c. 1.7 Ma saw a mirrored temporary increase in woodland vegetation, and marked a transition to more variable, likely seasonal, vegetation cover. Although mosaic habitats would have supported habitat generalists and specialists alike, the inferred environmental instability for the Cradle of Humankind broadly coincides with the Oldowan-Acheulean transition.

12.5 IMPACT OF CLIMATE AS AN EVOLUTIONARY DRIVER IN SOUTHERN AFRICA

The southern African hominin landscapes are dynamic (Dirks and Berger 2018) but lack the active faulting prevalent in East African hominin contexts. It would be logical that both climate and geology impact upon the vegetation a landscape is capable of supporting and subsequently upon habitat preference for the entire faunal community. Repeated plant succession with a greater prevalence of pioneer species may be anticipated for more tectonically active locales, providing relatively little in the way of shelter. Yet slightly removed from the epicentres of tectonic activity, the resultant palaeolakes created and the vegetation structure supported can be vast, creating and maintaining preferential hominin and faunal habitat types. The vegetation around the hominin sites around the Cradle of humankind were undoubtedly affected by such landscape dynamics but arguably to a lesser extent than was the case in East Africa. It is

therefore suggested that other factors, including the impact of climate is likely to be a more influential factor in South Africa than in East Africa. Thus, research can address the impact of climate as an evolutionary driver with more certainty.

Hypothesis	Proposed environmental and vegetation change according to climatic	*Antidorcas* evidence
SH (savannah hypothesis) (Dart 1925)		Yes the general trend towards increasing aridity prevails but with a temporary patch of environmental instability and habitat heterogeneity c. 1.7 Ma.
TPH (turnover pulse hypothesis) (Vrba 1985)		No major 'pulses' are evidenced in relation to faunal turnover but c. 1.7 Ma, habitat heterogeneity and environmental instability are inferred. This is inferred to be linked to the oWC. Stasis is not inferred in between climatic events but rather, gradual adaptation and evolution.

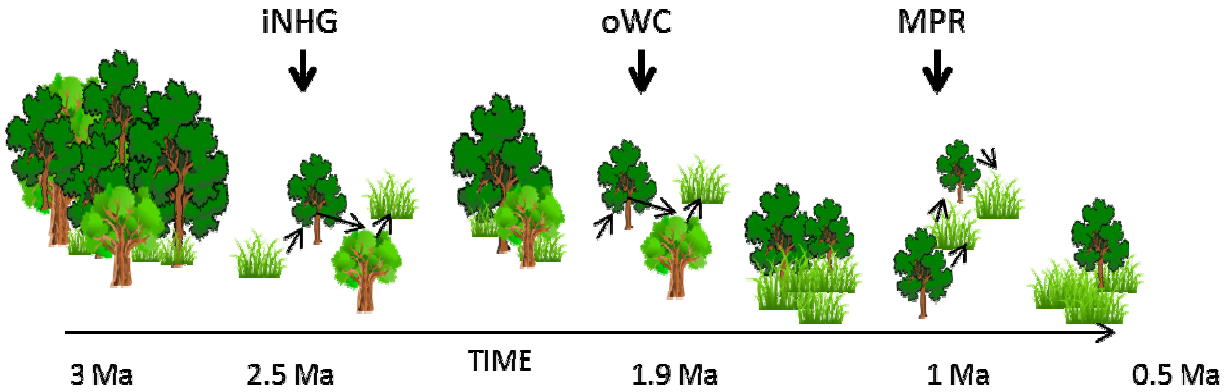
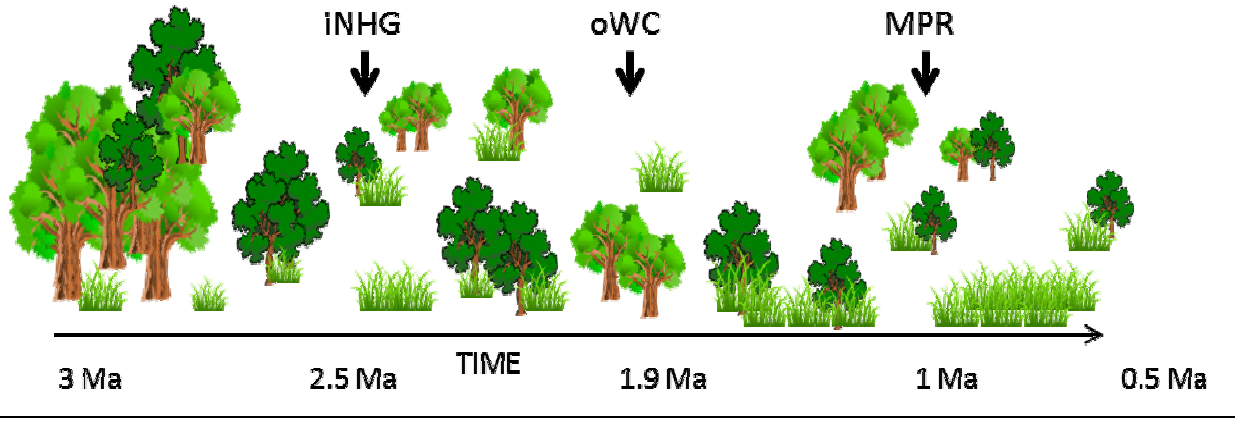
VSH (variability selection hypothesis) (Potts 1998)		Yes, habitat heterogeneity and environmental variability evidenced via intra and inter specific variability is inferred c. 1.7 Ma, causally linked to the oWC. The enhancement of seasonal changes impacts upon the *Antidorcas* diet.
MHM (mosaic habitat model) (Reynolds et al. 2015)		Yes, mosaic habitats are available throughout for *Antidorcas* to utilise but with an underlying trend towards increased aridity. The climatic changes associated with the oWC lead to temporarily increase habitat heterogeneity.

Figure 12.4: Antidorcas evidence compared to climate-related evolutionary theories.

A combination of all these evolutionary theories (Figure 12.4) can be seen throughout this temporal range in South Africa, with the more local scale changes acting to buffer/ enhance larger scale impacts for the Cradle of Humankind *Antidorcas*. *Antidorcas* species are able to survive via dietary flexibility. Intra-specific dietary variability increases as a result of proposed climatic events and their inferred impact of environmental instability. This is particularly evident for the oWC (onset of the Walker Circulation) which saw increased seasonality and likely marks the increase in seasonal mixed feeding for *Antidorcas*.

12.5.1 Global context

This section addresses whether the trends found via *Antidorcas* at the Cradle of Humankind sites mirror those seen for hominin landscapes elsewhere during this time period.

12.5.1.1 Contemporary Europe

The onset of the glacial cycles and increased seasonality associated with the iNHG c. 2.6 Ma were readily apparent via European bison intra-tooth oxygen isotopic composition (Bernard et al. 2009). Later, species diversity and variable environmental habitats have been suggested during the earliest appearance of *Homo* in Europe (c. 2.1-0.4 Ma) (Sardella et al. 2018) as well as marked seasonality (Strani et al. 2018).

12.5.1.2 Africa

Potts (1996, 1998, 2013) promotes a theory of high climate variability during key hominin evolutionary events, such as FADS/ LADS in East Africa. Leaf wax biomarkers show environmental variability and instability c. 1.9-1.4 Ma in West Turkana (Lupien et al. 2018). Particularly high amplitude in hydrological variation is apparent c. 1.7 Ma, coincident with the emergence of *H. erectus* (*senso lato*) and the appearance of Acheulean technology, implicating the importance of climatically-driven hominin evolution (Lupien et al. 2018). Whilst the same resolution of climate in relation to hominin (or *Antidorcas*) evolution cannot yet be achieved for South Africa, environmental instability is suggested here across the Oldowan-Acheulean transition. This transition saw the appearance of South African Homo and the behavioural advancements associated with the Acheulean lithic technology c. 1.7 Ma.

Across this transition in Olduvai Gorge, East Africa, avifauna supports a general opening and drying of the landscape, increasingly supporting grasslands and open woodland (Prassack et al. 2018). Similarly, c. 1.7 Ma, dietary differences in the most abundant bovids (including *A. recki*) were interpreted as seasonal differences in time of death for individuals but no major dietary or hydroclimatic change (Rivals et al. 2018). Rivals et al. (2018) also served to highlight the importance of using multiple proxies to detect both long- and short-term environmental change to understand the context within which hominins evolved. Large mammal evidence also does not support major vegetation or hydrological change but does show stronger seasonal dietary differences for some taxa across the Oldowan-Acheulean transition (Uno et al. 2018).

12.5.1.2.1 Southern Africa

2.7 Ma: Intensification of Northern Hemisphere Glaciation (iNHG)

A. bondi significantly altered its lifetime diet from Sterkfontein Member 4 to Kromdraai W (mesowear), which is likely representative of this transitional period. However, no other

evidence supports major palaeovegetation change resulting from the iNHG around the Cradle of Humankind.

2.0-1.7 Ma: Onset of the Walker Circulation (oWC)

The general trend through this temporal range is of increased aridity and relative grasslands, with increased habitat heterogeneity, temporarily wetter with an increase in woodland habitats c. 1.7-1.07 Ma, (Swartkrans M2 and Sterkfontein M5).

The *Antidorcas* evidence supports climatically-driven behavioural (dietary) change. Additionally, some subtle adaptive responses in *Antidorcas* dentition are apparent, as a result of dietary changes in response to altered vegetation cover and habitat availability within the landscape.

Antidorcas bondi's increase in cusp height (measurements) and browsing (mesowear) evident post 1.7 Ma (Swartkrans Member 2 and Sterkfontein Member 5) supports the notion of vegetation change and selective pressures acting upon the faunal community as a response to environmental conditions of the time, implicating the oWC.

In spite of the likely time-averaged deposition prevalent at the sites represented, unless significantly differentially averaged across deposits of the same site, Sterkfontein Member 5 and Swartkrans Member 2 show considerably greater levels of intra-specific variation.

Environmental instability, with a dominant temporary decrease in aridity and increase in C_3 browse-type vegetation, is inferred for this temporal range by high intra-specific diversity in dental measurements and use-wear (mesowear and microwear) signals from all *Antidorcas* species. As *A. recki* shows a slight increase in grazing (microwear) from Sterkfontein Member 4 to Kromdraai (W) and Sterkfontein Member 5, it is suggested that although temporarily wetter, with less grassland prevalence and habitat heterogeneity, the underlying general trend towards increased aridity and grassland dominance from Sterkfontein Member 4 still prevails.

The Oldowan-Acheulean transitionary period within the Cradle of Humankind from this evidence, is inferred to have consisted of environmental instability with high habitat heterogeneity across the landscape.

1.0 Ma: Mid-Pleistocene Revolution (MPR)

A long-term aridification, with marked precessional variability, around the Cradle of Humankind (Limpopo catchment) between 1.0-0.6 Ma was evidenced via a multiproxy reconstruction of hydrological changes (Caley et al. 2018).

Similar to hominins, *Antidorcas* can be inferred to have been eurytopic (capable of withstanding environmental variability). Yet the preferred habitats of both *A. recki* and *P. robustus* gradually became scarcer post 1 Ma, following the trend of increased aridity and grassland dominance, leading to the demise of both *A. recki* and *P. robustus*. *Antidorcas* is likely to have been subject to turnover (*A. recki* extinction) following this marked trend and the impact of precessional variability. Additionally, Plovers Lake *Antidorcas* supports a temporary increase in intra-specific variability in dental measurements. *A. bondi* however, appears to be consuming more browse post 1.0 Ma. This trend has been noted elsewhere in South Africa, albeit not exclusively, for *A. bondi* (Codron et al. 2008; Adams et al. 2013; Brink et al. 2012) and perhaps suggests a biological cause, being out-competed by more

specialized grazers; or an abiotic cause, being unable to withstand the increasing temperatures perhaps due to more intangible traits, seeking more sheltered, browse-dominated habitat.

12.6 ADDRESSING THE RESEARCH QUESTIONS

1) What was the prevailing landscape vegetation cover and aridity like in southern Africa between 2.8-0.8 Ma?

From woodland-dominated landscapes of 2.8 Ma, mixed-mosaic habitats became dominant and were available throughout the landscape for the rest of the duration of this temporal range. A gradual increase in aridity and grassland availability from 2.8 to 0.8 Ma is apparent with a temporary increase in woodland habitats and decrease in aridity occurred c. 1.7 Ma (predominantly evident from Swartkrans Member 2).

2) What was the extent and tempo of vegetation change? Do these changes relate to known global climatic trends and events (i.e. are *Antidorcas* affected by any of these major climatic changes?) Are there any major evolutionary events or dietary shifts seen in the *Antidorcas* lineage (are there obvious turnovers within the *Antidorcas* lineage)?

From all of the *Antidorcas* evidence combined (dietary, dental morphology and aridity indicators), vegetation change appears to have occurred gradually, with periods of increased variability occurring at differing magnitudes. A marked period of instability is evident c. 1.7 Ma, during which there was increased habitat heterogeneity, causing *Antidorcas* to display varying lifetime diets and high intra-specific dietary variability.

The *Antidorcas* lineage (as defined in the glossary), does experience turnover. *Antidorcas recki* appears to speciate into *Antidorcas marsupialis* ~1.7 Ma. Caution is exercised before inferring climatic catalysts here due to the nature of cave stratigraphy with its inherent time-averaging. Moreover, the differential identification of early *A. marsupialis* from late *A. recki* is not an easily achieved. *A. recki* appears to co-inhabit alongside *A. marsupialis* and *A. bondi* until ~ 1 Ma. Character displacement between *Antidorcas* species is apparent throughout this temporal range (see Figure 12.1).

3) Palaeoecology of the *Antidorcas* species

A. bondi is found in greatest abundance in Swartkrans Member 2, which unexpectedly shows increased woodland dominance and decreased aridity compared to other members. From c. 1.7 Ma (around Swartkrans Member 2), *A. bondi* displays more individual variation within species and more lifetime (seasonal-type) mixed feeding. Although many *A. bondi* individuals conform to the typical diet of *A. bondi* as a grazer, many do not. Overall, *A. bondi* is a variable mixed-feeder throughout this temporal range but this dietary tendency increases through time. Some individuals are obligate grazers, some obligate browsers and others are practicing mixed-feeding throughout their lifetime, likely seasonally. *A. bondi* typically have more variation in their lifetime diet when compared to the other fossil *Antidorcas* species. Overall, *A. bondi* presents as a likely seasonally migrating species.

A. recki is predominantly a browsing species but also shows evidence of mixed-feeding, with an increase in mixed-feeding tendencies through time.

A. marsupialis is a mixed-feeding species throughout with the suggestion of increasing C_3 component of its diet through time. Mixed-feeding in *A. marsupialis* is typically mixed-feeding (opportunistically) throughout its lifetime with no consistent difference between early years, lifetime diet and end of life diet.

From their dental remains, no evidence was found to support the Cradle of Humankind specimens identified as '*A. australis*' being a separate species.

Antidorcas, as generalists appear to be progressively pushed into more mosaic habitats, likely by specialist grazing species as grassland habitats become increasingly prevalent across the landscape through time.

4) What can *Antidorcas* information gained here add to the hominin story?

Antidorcas (as a bioproxy for vegetation change) evidence gained here supports the trend for increased aridity through time (via oxygen isotope values and inferred character displacement) and the suggestion of environmental change c. 1.9-1.7 Ma, in line with terrestrial evidence for climatic change (e.g. speleothem data- Hopley et al. 2007a, b). This supports the theories such as environmental variability-hypotheses (Potts 1996; Potts and Faith 2015; Maslin et al. 2015) and the influence of climate as an evolutionary driver across the Oldowan-Acheulean transition in South Africa.

Antidorcas is a good bioproxy if the limitations of using a water-independent, mixed-feeding genus are acknowledged and mitigated for. Its abundance in many hominin-bearing deposits is of use in ensuring sufficiently large sample sizes are achievable to yield conclusive results. Providing the research questions incorporate what is achievable from this mixed-feeding genus, their use as a palaeoenvironmental indicator would also be of benefit to inform on hominin contexts elsewhere.

12.6.1 Assessing the role of climate as an evolutionary driver

From the *Antidorcas* evidence researched here, the role of climate as an evolutionary driver is dependent on regional and local buffers, the degree of dietary and habitat specialism of the taxa under study, and the magnitude and longevity of the climatic event / change. The climatic catalyst needs to be sufficiently strong, with consequent prolonged environmental instability to initiate sufficient regional and local environmental change capable of percolating down to the habitat level. If so, climate is capable of causing selection pressure and inducing adaption and evolution upon the faunal communities, *Antidorcas* and hominins alike. From the *Antidorcas* evidence, the initiation of seasonal diversification associated with the onset of the Walker Circulation (c.1.7 Ma) had the most impact, both temporarily during its initiation and longer-term as a result of the directional change caused.

12.7 CONCLUSION

All *Antidorcas* species have variable mixed–feeding diets during this temporal range 2.8-0.8 Ma. The underlying trend of gradually increasing aridity is evident but with mosaic habitats available throughout. *Antidorcas*, as a (generalist) flexible feeder is able to shift its diet to enable survival during periods of environmental instability, such as is suggested for

~ 1.7 Ma and likely pushed into more mosaic habitats by increasing grassland-specialists as grassland habitats expand. The onset of the Walker circulation (c. 1.9-7 Ma) causing climatic shifts (El Niño and la Niña events) marked an increase in seasonal dietary practice for *Antidorcas*, evidenced via varying lifetime diets. A temporary period of increased habitat heterogeneity, as a result of the onset of the Walker circulation and a shift of orbital forcing dominated by obliquity periodicity (40kys), is inferred from increased dietary variability ~ 1.7 Ma in the Cradle of Humankind. This supports the dietary flexibility suggested for hominins capable of withstanding and adapting to regional and local environmental variation. However, the larger scale global influence with associated environmental instability and enhanced seasonality evident around the Oldowan-Acheulean transition creates sufficient habitat change across the landscape to catalyse change.

FUTURE WORK

A selection of modern and fossil *Antidorcas* have been sampled for phytoliths. The analysis of which can be combined with the results from this research to produce a more comprehensive palaeovegetation picture with direct botanical evidence (if present).

Knowledge of the migration of African fossil bovids would assist in detangling the seasonal resident and, or variable mixed-feeding pattern from evidence of migration, e.g. via a combination of stable isotope analysis (adding strontium analysis) with DMTA and mesowear.

Further taxonomic investigation of the *Antidorcas* genus would be beneficial to establish a comprehensive evaluation. Geometric morphometrics of dentition, alongside postcranial and horncore material would provide a more holistic taxonomic identity for each species. This would enable researchers to better quantify taxonomic differentiation of *Antidorcas* species.

Further to this, a direct comparison with the '*A. australis*' specimens considered here with Cape specimens would provide more conclusive evidence in regards to the taxonomic identity and rank of this proposed species (Hendey and Hendey 1968).

Finally, to enhance the somewhat muted story obtained from this research, a comparison of the same in-depth multi-method research could be conducted using obligate grazers and browsers from the same assemblages. They would strengthen the findings here as whilst these obligate dietary species may be only intermittently present, when combined with this *Antidorcas* (continuously present but mixed-feeding) signal obtained here, a complete palaeoenvironmental picture is achievable.

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